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THE UNIVERSITY OF ALBERTA

DIFFERENTIAL PREDATION UPON EMBRYOS AND LARVAE OF TEMPERATE PACIFIC ECHINODERMS

by

STEVEN SEWARD RUMRILL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY.

EDMONTON, ALBERTA

Fall 1987

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17 Sept. 87

Dear Steve,

You have my full consent to use part or all of our collaborative publication as a chapter of your Ph.D. thesis. The publication is entitled "Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz) embryos and larvae by zoeae of the red crab *Cancer productus* Randall.

With Best Regards,

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Dear Steve:

Thanks for bringing to the topic of jointly-authored publications to my attention. You have my full consent to use part or all of our collaborative publication in your thesis. The article is entitled "Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz), embryos and larvae by zoeae of the red crab, *Cancer productus* Randall".

I hope we will have the opportunity to collaborate again.

Sincerely,

Dr. J. Timothy Pennington

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DATED 17 September 1987

"Just inside the deep fjord called Barclay Sound (sic). Quiet waters but with plenty pelagic larvae of surfswept animals, to be sorted out by the environment and by the physiological needs of the beasts themselves, and by eating and being eaten. That sorting out is a curious process."

Ed Ricketts (1945)
The Outer Shores. Part 1. Ed Ricketts
and John Steinbeck Explore the Pacific
Coast. J. W. Hedgpeth, ed. Mad River
Press. Inc. (1978)

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled DIFFERENTIAL PREDATION UPON EMBRYOS AND LARVAE OF TEMPERATE PACIFIC ECHINODERMS submitted by STEVEN SEWARD RUMRILL in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Date 18 September 1987

ABSTRACT

A fundamental premise of benthic marine invertebrate life history theory asserts that energetic costs associated with lecithotropic and brooding modes of development are offset by decreased rates of mortality during periods of embryo and larval development. These energetic tradeoffs are presumably the basis for the evolution of dichotomous modes of development among several invertebrate taxa, and they provide the foundation for an inverse correlation between fecundity and offspring survivorship.

In this thesis, I describe a series of experimental observations to test the hypothesis that rates of embryo and larval mortality are inversely correlated with initial egg size and mode of development. Tests of hypotheses rely primarily upon comparisons made in the laboratory among echinoderm larvae from the Pacific Northwest. The life history patterns and differential susceptibility of planktotrophic and lecithotrophic larvae to predation by carnivorous zooplankton support the size-mortality hypothesis, although stage-specific differences in embryo and larval susceptibility were found to vary substantially among species with planktotrophic and lecithotrophic modes of development. Microcosm feeding experiments demonstrate stage-specific differences in the susceptibility of echinoderm embryos and larvae to predation by carnivorous zooplankton. The occurrence of similar stage-specific susceptibility curves among phyletically divergent types of echinoderm larvae, and among different types of predatory zooplankton, allow predator-prey interactions to be assessed at a functional-group level that recognizes five distinct patterns of larval susceptibility. The fixed shapes of stage-specific susceptibility curves at various temperatures suggests that cumulative losses of embryos and larvae to predation are directly related to rates of larval development in nearshore waters.

Ontogenetic changes in the behavior of echinopluteus larvae can be an effective deterrent to predation by brachyuran zoeae. In contrast, the swimming behavior of asteroid larvae increased their probability of capture by two species of benthic suspension feeders. These investigations highlight the importance of larval behavior at low Reynolds numbers. Differences in the field distribution of juvenile asteroids, coupled with information from zooplankton tows and laboratory feeding and substratum selection experiments, support the hypothesis that communities of benthic suspension-feeders can influence the survivorship of echinoderm larvae during settlement.

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attributes will continue to make Bamfield an attractive site for future studies of invertebrate embryology and larval ecology. I am also grateful to D. Boag, R. Peter, and A. Spencer (University of Alberta, Department of Zoology), G. Kaplan, (Vice President of Reseach), and the Faculty of Graduate Studies and Research for the provision of funds that allowed me to travel to international meetings in Ireland and England; conversations with colleagues at these times provided a much needed break from field work and served ultimately to shape some of the ideas presented in the dissertation.

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Table of Contents

Chapter Page

I GENERAL INTRODUCTION 1
- A. LIFE HISTORY TRAITS OF BENTHIC MARINE INVERTEBRATES 2
- B. ESTIMATION OF LARVAL MORTALITY RATES 4
- C. SOURCES OF LARVAL MORTALITY 8
- D. PRIMARY OBJECTIVES OF THE RESEARCH 14
- E. APPLICABILITY OF ECHINODERM EMBRYOS AND LARVAE 15
- F. ORGANIZATION OF THE THESIS 18
- G. LITERATURE CITED 21

II DIFFERENTIAL SUSCEPTIBILITY OF MARINE INVERTEBRATE LARVAE: PREDATION UPON _Dendraster excentricus_ (ECHINOIDEA: CLYPEASTEROIDA) EMBRYOS AND LARVAE BY ZOEAE OF THE RED ROCK CRAB _Cancer productus_ (CRUSTACEA: DECAPODA) 32
- A. INTRODUCTION 32
- B. MATERIALS AND METHODS 35
  - 1. Larval Abundance 35
  - 2. Functional Response of _Cancer_ Predation .. 35
  - 3. Differential Susceptibility of Embryos and Larvae 37
  - 4. Post-Contact Encounter Response 40
- C. RESULTS 41
  - 1. Larval Abundance Patterns................. 41
  - 2. Functional Response of _Cancer_ predation .. 42
  - 3. Differential Susceptibility of Embryos and Larvae 42
  - 4. Post-Contact Encounter Response.......... 53
- D. DISCUSSION.................................. 56
  - 1. Size-Selective Predation 56
  - 2. Larval Morphology 58
  - 3. _Dendraster_ Motility 59
  - 4. _Dendraster_ Swimming Behavior 60
- E. LITERATURE CITED............................ 64

III EFFECTS OF OVA SIZE, DEVELOPMENT RATE, AND AMBIENT TEMPERATURE ON THE EARLY MORTALITY OF PLANKTOTROPHIC ECHINODERM LARVAE 70
- A. INTRODUCTION 70
- B. MATERIALS AND METHODS 72
  - 1. Study Organisms 73
  - 2. Measurements of Ova Size 74
  - 3. Effects of Temperature on Development Rates 74
  - 4. Predation by Zooplanktonic Crustaceans ... 75
- C. RESULTS 78
  - 1. Variation in Ova Size 78

2. Effects of Temperature on Development Rates 80
3. Predation by Zooplanktonic Crustaceans ... 85
a. Functional Response of Predation 86
b. Stage-Specific Susceptibility 86
c. Long-Term Predation Experiments 100
D. DISCUSSION 112
E. LITERATURE CITED 119

IV LOCOMOTION AND PREY CAPTURE BY ZOEA LARVAE OF THE KELP CRAB, _Pugettia_ _producta_ (DECAPODA: BRACHYURA: MAJIDAE) 122
A. INTRODUCTION 122
B. MATERIALS AND METHODS 124
1. Rearing of Larvae....................... 124
2. Hydromechanics of Swimming 124
3. Hydromechanics of Particle Capture 127
C. RESULTS 127
1. Swimming Behavior of _Pugettia_ _producta_ zoeae 127
2. Velocity and Acceleration Profiles 131
3. Morphology of the Swimming and Feeding Appendages 145
4. Hydromechanics of Swimming 148
5. Capture of Prey Items 158
D. DISCUSSION 162
1. Locomotion of _Pugettia_ zoeae 163
2. Prey Capture by _Pugettia_ zoeae 168
3. Comparison between Brachyuran Zoeae and other Aquatic Arthropods 170
4. Importance of the Acceleration Reaction .. 174
E. CONCLUSIONS 178
F. LITERATURE CITED 180

V RECRUITMENT OF _Asterina_ _miniata_ (BRANDT, 1835): A POST-FACTO ASSESSMENT OF LARVAL ABUNDANCE, SUBSTRATUM SELECTION, AND LARVAL PREDATION 187
A. INTRODUCTION 187
B. MATERIALS AND METHODS 191
1. Study Sites 191
2. Abundance and Recruitment of _Asterina_ 191
3. Reproductive Activity of _Asterina_ 195
4. Larval Distribution and Abundance 195
5. Larval Substratum Selection 196
6. Predation upon Larvae by Benthic Suspension Feeders 198
a. Analysis of Gut Contents 198
b. Laboratory Predation Experiments 199
c. Predator Encounter Rates 202
7. Juvenile Survivorship 204
8. Juvenile Immigration and Emigration 205

C. RESULTS 205
  1. Study Sites 205
  2. Abundance and Recruitment of _Asterina_ 206
  3. Reproductive Activity of _Asterina_ 212
  4. Larval Distribution and Abundance 217
  5. Larval Substratum Selection 223
  6. Predation upon Larvae by Benthic Suspension Feeders 229
    a. Analysis of Gut Contents 232
    b. Laboratory Predation Experiments 237
    c. Predator Encounter Rates 247
  7. Juvenile Survivorship 261
  8. Juvenile Immigration and Emigration 266
D. DISCUSSION 268
  1. Reproductive Activity of _Asterina_ _miniata_ 268
  2. Spatial Heterogeneity of Larval Populations 269
  3. Substratum Selection by _Asterina_ Brachiolaria Larvae 272
  4. Predation upon Larvae During Settlement .. 276
  5. Survivorship of Post-Larvae and Juveniles 283
  6. Immigration and Emigration following Settlement 285
  7. Conclusions 292
E. LITERATURE CITED 295

VI STAGE-SPECIFIC MORTALITY OF MARINE INVERTEBRATE LARVAE: GENERAL CONCLUSIONS AND IMPLICATIONS FOR LIFE HISTORY THEORY 309
A. INTRODUCTION 309
B. MATERIALS AND METHODS 310
  1. Intensive Sampling of Larval Populations . 311
  2. Differential Susceptibility of Echinoderm Larvae 311
C. RESULTS AND DISCUSSION 312
  1. Intensive Sampling of Larval Populations . 312
  2. Differential Susceptibility of Echinoderm Larvae 325
  3. Implications for Life History Theory 333
  4. Contributions to the Study of Larval Mortality 335
  5. Recommendations for Future Research 339
D. LITERATURE CITED 341

APPENDIX I. SMALL-SCALE BIOGEOGRAPHICAL VARIATION IN LIFE HISTORY DIVERSITY AMONG ECHINODERM FAUNAL ASSEMBLAGES FROM BARKLEY SOUND, BRITISH COLUMBIA 343
A. INTRODUCTION 343
B. MATERIALS AND METHODS 345
  1. Description of Study Areas 345

    2. Surveys of Benthic Transects 355
    3. Echinoderm Life History Traits 358
    4. Large-Scale Shifts in Echinoderm Life History Traits 359
C. RESULTS 359
    1. Comparison of Study Areas 359
    2. Diversity and Abundance of Echinoderms ... 368
    3. Echinoderm Life history Traits 390
    4. Relationships Between Species Diversity, Life History Traits, and Distribution 400
D. DISCUSSION 413
E. LITERATURE CITED 423

APPENDIX II. 431

List of Tables

Table — Page

1 Categories of *Dendraster excentricus* prey used in feeding experiments and their characteristic shapes, sizes and motility 38

2 Vertical abundance of echinoid larvae and brachyuran crab zoeae by depth stratum in Barkley Sound, British Columbia 43

3 Summary of clearance rates during predation upon variously treated *Dendraster excentricus* plutei by *Cancer productus* zoeae 52

4 Comparison of the diameters and volumes of naturally spawned ova from seven species of echinoderms 79

5 Predation rates by *Pugettia producta* zoeae upon embryos and larvae of seven planktotrophic echinoderms during long-term feeding experiments 105

6 Comparison of correlation coefficients for relationships between mortality, ova volume and development rate to a feeding larval stage . 109

7 Comparison of morphological features between stage I and stage II zoea larvae of *Pugettia producta* 132

8 Comparison of linear dimensions, velocities and Reynolds numbers for zoea larvae and various appendages 149

9 Developmental stages of *Asterina miniata* used in feeding experiments with *Pachycerianthus fimbriatus* and *Corella willmeriana* 200

10 Seasonal estimates of ray length, density and percentage of monthly population samples for age-1 and age-2 cohorts of *Asterina miniata* at the Grappler Inlet study site 211

11 Schedule of development for *Asterina miniata* embryos and larvae in laboratory cultures 218

12 Vertical stratification of asteroid larvae in Trevor Channel 219

13 Metamorphosis of *Asterina miniata* in the multiple substratum settlement experiment 224

14 Metamorphosis of *Asterina miniata* in single substratum experiments 228

15 Metamorphosis of *Asterina miniata* in the sediment aging experiment 230

16 Densities of benthic suspension feeders in Bamfield and Grappler Inlets 231

17 Summary of Student-Newman-Keuls tests of differences in capture frequencies between developmental stages of *Asterina miniata* 240

18 Results of single-factor ANOVA tests of the effects of prey density on predation rates upon *Asterina embryos* and larvae 244

19 Filtration efficiencies of *Corella* and *Pachycerianthus* during flow tank feeding experiments 246
20 Definitions and units of symbols used in equations 1-8 253
21 Percentage of juvenile *Asterina miniata* consumed by *Pycnopodia helianthoides* in a laboratory aquarium 265
22 Crawling speeds of *Asterina miniata* post-larvae and juveniles 267
23 Comparison of laboratory and field growth rates of *Strongylocentrotus droebachiensis* echinopluteus larvae 319
24 Summary matrix of predator-prey experiments conducted with 34 species of planktivorous invertebrates and fish and 17 species of echinoderms 326
25 Comparison of study areas, habitats and vertical ranges sampled by benthic transect lines at the Taylor Island, Bamfield and Grappler Inlet sites 348
26 Comparison of the relative positions of 17 benthic transect lines along the environmental gradient 365
27 Population densities of echinoderms along 5 transect lines at Taylor Island 378
28 Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets 381
29 Comparison of larval trophic modes, larval types, ova diameters, and maximum fecundities of echinoderms from Barkley Sound 391
30 Breeding seasons of echinoderms from Barkley Sound 396
31 Summary of comparisons between life history traits and species richness, diversity and exposure 402

List of Figures

Figure Page

1 Functional response of *Cancer productus* predation to abundance of *Dendraster excentricus* embryos 44

2 Clearance rates by *Cancer productus* zoeae upon various developmental stages of *Dendraster excentricus* during single-stage feeding experiments 47

3 Clearance rates by *Cancer productus* zoeae upon various developmental stages of *Dendraster excentricus* during mixed-stage feeding experiments 49

4 Camera lucida tracings of encounters between *Dendraster excentricus* gastrulae and echinoplutei and tethered *Cancer productus* zoeae 54

5 Development rates of echinoid embryos and larvae 81

6 Development rates of asteroid embryos and larvae 83

7 Functional responses of predation by *Parathemisto pacifica*, *Pugettia producta* and *Neomysis rayii* upon echinoid embryos 87

8 Functional responses of predation by *Parathemisto pacifica*, *Pugettia producta* and *Neomysis rayii* upon asteroid embryos 89

9 Functional responses of predation by *Parathemisto pacifica*, *Pugettia producta* and *Neomysis rayii* upon asteroid embryos 91

10 Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus* by *Pugettia producta* 94

11 Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus by Parathemisto pacifica* 96

12 Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus* by *Neomysis rayii* 98

13 Differential rates of predation upon developmental stages of *Strongylocentrotus purpuratus* and *Dendraster excentricus* by *Pugettia producta* 101

14 Differential rates of predation upon developmental stages of *Pisaster ochraceus* and *Orthasterias koehleri* by *Pugettia producta* . 103

15 Clearance rates of *Pugettia producta* zoeae during predation upon *Strongylocentrotus franciscanus* and *Pisaster ochraceus* embryos 107

16 Correlation between larval mortality and the duration of the high susceptibility (pre-feeding) period of development 110

17 The relationship between swimming velocity and carapace diameter for stage I and stage II zoea larvae of Pugettia producta 129
18 Velocity profiles for 6 stage I zoea larvae of Pugettia producta 133
19 Velocity profiles for 6 stage II zoea larvae of Pugettia producta 136
20 Instantaneous velocity and acceleration profile for a stage I zoea larva of Pugettia producta .. 139
21 Instantaneous velocity and acceleration profile for a stage I zoea larva of Pugettia producta .. 141
22 Instantaneous velocity and acceleration profile for a stage I zoea larva of Pugettia producta .. 143
23 Morphological traits of Pugettia producta zoeae 146
24 Movements of fluid and maxillipeds by tethered zoeae of Pugettia producta 151
25 Diagrammatic summary of the oscillation cycle of the 1st and 2nd maxillipeds 153
26 Relationship between the effective and recovery stroke cycles of the 1st and 2nd maxillipeds of a Pugettia producta stage I zoea 155
27 Feeding of Pugettia producta zoea larvae in moving fluid 159
28 Field sites in Barkley Sound, Vancouver Island, British Columbia 192
29 Seasonal surface temperature and salinity measurements from January 1984 to December 1985 207
30 Size-frequency distributions of Asterina miniata populations from March 1985 to February 1986 ... 209
31 Inferred growth of post-larvae and juveniles of Asterina miniata 213
32 Gonad and pyloric caecum indices for Asterina miniata from March 1985 to February 1986 215
33 Seasonal abundance of asteroid larvae at 3 zooplankton sample sites in 1985 221
34 Metamorphosis of Asterina miniata in single substratum experiments 226
35 Seasonal densities of benthic suspension feeders in Bamfield and Grappler Inlets in 1985 233
36 Size distribution of prey items recovered from gut contents of Corella willmeriana and Pachycerianthus fimbriatus 235
37 Mortality of various developmental stages of Asterina miniata during single-stage feeding experiments with benthic suspension feeders 238
38 Partial functional responses of suspension feeders to differences in the density of Asterina miniata prey stages 242
39 Transverse paraffin section through the branchial basket of Corella willmeriana 248

40 Capture of *Asterina miniata* bipinnariae by marginal tentacles of *Pachycerianthus fimbriatus* 250
41 Effect of current velocity on the dimensionless indices of larval capture Nmf and Nmp 254
42 Geometric reconstructions of the instantaneous volumes of water filtered by *Pachycerianthus fimbriatus* and *Corella willmeriana* 258
43 Graphical model of the pooled probabilities of predation upon brachiolaria larvae of *Asterina miniata* during settlement by *Corella willmeriana* and *Pachycerianthus fimbriatus* 262
44 Graphical model of the effects of vertical tiering in the community of benthic suspension feeders and larval searching behavior on the risk of predation during settlement of *Asterina miniata* in Bamfield Inlet 280
45 Daily variation in the density of echinoid larvae collected from shallow depths in Trevor Channel, Barkley Sound 314
46 Daily variation in the density and stages of *Strongylocentrotus droebachiensis* echinoplutei collected from shallow depths in Trevor Channel, Barkley Sound 317
47 Daily variation in the density of *Strongylocentrotus droebachiensis* echinoplutei collected from shallow and deep water in Trevor Channel, Barkley Sound 321
48 Differential susceptibility of echinoderm embryos and larvae 330
49 Location of study areas within Barkley Sound ... 346
50 Locations of 5 transect lines laid at Taylor Island 350
51 Locations of 12 transect lines laid within Grappler and Bamfield Inlets 352
52 Seasonal surface temperatures over 2 consecutive years at Taylor Island and within Bamfield and Grappler Inlets 360
53 Seasonal surface salinities over 2 consecutive years at the Taylor Island, Bamfield and Grappler Inlet study sites 363
54 Exposure gradient within Barkley Sound estimated by the proportional weight loss of plaster casts along 17 transect lines 366
55 Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Taylor Island study site . 369
56 Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Bamfield Inlet study site 371

57 Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Grappler Inlet study site 373
58 Proportions of the echinoderm fauna composed of echinoids, asteriods, holothuroids and crinoids 375
59 Comparison of 4 measures of echinoderm faunal diversity along 17 transects lines 387
60 Distribution of ova diameters among 36 species of echinoderms listed in Table 29 394
61 Diversity of echinoderm larvae among the Barkley Sound fauna 398
62 Shifts in the proportions of the echinoderm fauna composed of planktotrophic, lecithotrophic and brooding species along the exposure gradient at Taylor Island 403
63 Shifts in the proportions of the echinoderm fauna composed of planktotrophic, lecithotrophic and brooding species along the exposure gradient at Bamfield and Grappler Inlets 405
64 Relationship between ova diameter and the habitat where species reach their greatest abundance 409
65 Latitudinal shifts in the proportions of asteroid faunal assemblages composed of planktotrophic, lecithotrophic and brooding species along the north-east Pacific coast 411

CHAPTER I

GENERAL INTRODUCTION

Planktonic larval stages are an integral component of the complex life cycles exhibited by many species of benthic marine invertebrates (Wilbur, 1980). Recent theoretical and empirical studies have sought to clarify the role played by marine invertebrate larvae in determining the tempo and mode of evolutionary changes among benthic populations. For example, larval dispersion has been shown to affect the biogeographical distribution of species and reputedly to influence the maintenence of genetic heterogeneity (Scheltema, 1968, 1971, 1975, 1978, 1986; Gooch, 1975; Marcus, 1977; Levinton, 1980; Slatkin, 1981; Jablonski and Lutz, 1980, 1983; Hedgecock, 1982, 1986; Burton, 1983, 1986; Prince et al., 1987). In addition, patterns of larval availability and recruitment contribute to variation in the abundance and age structure of benthic populations (Yoshioka, 1982; Caffey, 1985; Connell, 1985; Gaines et al., 1985; Roughgarden et al., 1985; Levin, 1986). The conspicuous role played by larvae in these studies provides an indication that parameters associated with larval survivorship are central to our understanding of the local abundance patterns and persistance of benthic populations.

Comparative information about rates of larval mortality are also critical to analyses of the evolution of marine invertebrate life history traits. Since the sizes of invertebrate embryos are thought to be representive of their probablity of survival to metamorphosis (Vance, 1973a,b; Chia, 1974; Strathmann, 1977; Turner and Lawrence, 1979; Caswell, 1981; Lawrence et al., 1984), rates of larval mortality can be considered as a measure of adult reproductive investment (Christiansen and Fenchel, 1979). Furthermore, the body form and trophic mode of larvae have important implications concerning the duration of the planktonic period (Chia, 1974; Strathmann, 1980). Finally, larval body size and swimming behavior are paramount in determining encounter rates with predatory zooplankton (Gerritsen and Strickler, 1977; Greene, 1985). As a consequence, ontogenetic changes in larval body size and behavior are inherently linked with the probability of larval survival and with the relative risk of predator-induced mortality in nearshore marine habitats.

A. LIFE HISTORY TRAITS OF BENTHIC MARINE INVERTEBRATES

The conceptual basis for understanding the life history evolution of benthic marine invertebrates has developed along two primary avenues over the past several decades (see reviews by Stearns, 1976, 1977; Hines, 1986). Foremost among these has been the classification of reproductive patterns into a series of developmental modes that recognize planktotrophy, lecithotrophy, direct development, and viviparity as fundamentally different adaptations for the production of offspring (Thorson, 1946, 1950; Mileikovski, 1971; Chia, 1974; Jablonski and Lutz, 1983). A second perspective views contrasting life history adaptations in light of their evolutionary implications, energetic considerations, and demographic consequences (Cohen, 1968; Murphy 1968; Schaffer, 1974; Stearns, 1976, 1977; Caswell, 1981, 1982; Lawrence et al., 1984; Roughgarden et al., 1985). Although these conceptual avenues offer different vantage points to survey the findings of past and recent research, both approaches can be improved by a critical examination of several intrinsic assumptions.

Energetic considerations and mortality rates of planktonic invertebrate larvae are both fundamental components of contemporary life history models (Vance 1973a,b; Christiansen and Fenchel, 1979; Pechenik, 1979; Strathmann, 1977; Jackson and Strathmann, 1981; Grant, 1983). Mathematical expressions of invertebrate life history traits generally pivot upon 1) differences in parental energetic investment per offspring, and 2) rates of planktonic mortality. The assumption that variability in the sizes of ova reflect differences in parental investment has recently been scrutinized by Turner and Lawrence (1979), Lawrence et al. (1984), McEdward and Coulter (1987), and McEdward and Carson (1987). Their findings indicate that intraspecific differences in ova diameter can be a poor indicator of energetic content in echinoderms with variable ova sizes. As a consequence, attempts to infer differences in reproductive investment from estimates of ova size alone may be seriously misleading.

B. ESTIMATION OF LARVAL MORTALITY RATES

Current theoretical arguements typically incorporate a larval mortality function that is based on little or no empirical data. Planktonic mortality rates are generally considered to be high in species with long-lived, planktotrophic larval stages. Conversely, mortality rates are generally assumed to be lower in species with shorter-lived lecithotrophic larvae or benthic development. In general, there have been three approaches to estimating characteristics of the larval mortality function. Simplistic models such as those of Vance (1973), Strathmann (1977) and Grant (1983) estimated larval mortality rates to be constant and high for all developmental stages of feeding and non-feeding planktonic larvae. In contrast, Christiansen and Fenchel (1979) and Ayal and Safriel (1982) proposed that planktonic mortality rates may be greater for younger larvae than older larvae, and they incorporated decreasing mortality functions into their models of returns on reproductive effort. A more recent approach (Emlet *et al.*, 1986) estimates the ratio of planktonic mortality rates necessary to balance the high fecundity of planktotrophic species with the lower fecundity of lecithotrophic species. However, like Menge (1975), Emlet et al. (1986) make the assumption that larval populations exist at equilibrium densities and that the risk due to predation is distributed equally among various developmental stages.

Non-empirical assessments of instantaneous larval mortality rates are of limited value in the analysis of field data because most field situations are too complex to allow for meaningful predictions. For example, non-empirical estimates of larval mortality cannot take into account important local conditions including temporal and spatial differences in larval production, advective and diffusive transport, larval growth rates, qualitative and quantitative differences in food availability, and the distribution and abundance of predatory zooplankton.

Attempts to monitor natural populations of planktonic larvae are beset by serious methodological problems that challenge the creativity of field-oriented ecologists. Consequently, many investigators have sought alternative methods to obtain estimates larval survivorship. A parsimonious approach has been to avoid the difficulty of estimating planktonic mortality by conducting periodic examinations of egg masses in species with benthic development (Spight, 1975; Menge, 1975; Shimek, 1981; Race, 1982; Wilson, 1986). Rates of larval mortality have also been estimated from time-series collections of zooplankton samples (Jørgensen, 1981; Rothlisbeg and Miller, 1982) and from differences between apparent larval production and recruitment (Thorson, 1950; Connell, 1970; Menge, 1975; Hines, 1979; Brousseau et al., 1982; Powell et al., 1984). Although they provide a first approximation of mortality rates, these indirect methods rely upon unreasonable assumptions concerning the density and age-stability of larval and adult populations, stage-specific differences in mortality, and rates of advective and diffusive larval transport. Despite the widespread ecological and evolutionary implications that derive from differential rates of larval mortality, few investigators have adequately addressed the fundamental assumptions that form the basis for comparative assessments.

Are marine invertebrate larvae exposed to a high risk of mortality due to the effects of predators? This question has been at the focal point of a controversy that laboratory experiments and non-empirical estimates of instantaneous larval mortality rates have failed to resolve. The prevalent view was first advanced by Thorson (1946, 1950) whose anecdotal observations suggest that predation upon larvae may be a paramount factor leading to large-scale losses of larvae from the plankton (Thorson, 1966). The hypothesis that marine invertebrate larvae are highly susceptible to predation has recently been substantiated in a series of laboratory experiments by Pennington and Chia (1984), Rumrill and Chia (1985), Rumrill et al. (1985), and Pennington et al. (1986). These studies document stage-specific differences in the susceptibility of larvae to predation, and they indicate that field mortality rates can be dependent upon the expression of larval traits and the feeding behavior of predatory zooplankton.

In contrast, alternative arguements express the opposing view that marine invertebrate larvae migrate into the plankton during early development to obtain food and to seek refuge from benthic predators (Jagersten, 1972; Strathmann, 1985). Implicit in the "safety-and-feeding" hypothesis is the assumption that feeding larvae are less vulnerable to predators than non-feeding larvae (Highsmith, 1985). However, planktotrophic larvae typically differ from lecithotrophic larvae in several fundamental traits including initial body size and morphology, patterns of ciliation, and swimming behavior. All of these characteristics are potentially significant in determining the relative susceptibility of larvae to capture by predatory zooplankton.

The "high-susceptibility" and "safety-and-feeding" hypotheses are not mutually exclusive. For example, it is possible that marine invertebrate larvae are exposed to a high risk of predator-induced mortality during the planktonic period, and that risk increases as larvae approach the bottom prior to settlement. Detailed studies of predator-prey interactions must be completed to determine the relative significance of planktonic and benthic rates of larval mortality.

In order to obtain accurate estimates of the mortality rates of marine invertebrate larvae, it is necessary to simultaneously evaluate several potentially synergistic parameters that contribute to larval losses. Accurate estimates of larval mortality must consider: 1) advective immigration and emigration of larval populations, 2) input of new individuals by spawning, 3) rates of larval feeding and growth, 4) stage-specific differences in the susceptibility of embryos and larvae, 5) density-dependent predation by zooplankton, and 6) rates of larval settlement. To my knowledge, studies are not available that adequately examine this suite of factors for any population of marine invertebrate larvae. Consequently, little convincing evidence exists to either support or refute the hypothesis that larval mortality is a selective agent in the evolution of invertebrate life history traits.

C. SOURCES OF LARVAL MORTALITY

Larvae of benthic marine invertebrates risk mortality from several different sources during the planktonic period. In his pioneering studies of invertebrate larval ecology, Thorson (1946, 1950, 1966) considered the major sources of loss to be: 1) failure of fertilization, 2) poor food supplies, 3) inadequate thermal conditions, 4) the absence of a proper substratum for metamorphosis, 5) offshore transport by currents, and 6) predation upon embryos and larvae.

The effects of genetic abnormalities and larval diseases are two potentially important and yet virtually unexplored sources of embryo and larval death. Large numbers of embryos and early larval stages often fail to develop in synchrony with their siblings in laboratory cultures, and these individuals are typically discarded by researchers. It is possible that a substantial proportion of siblings possess genetic abnormalities that result in aborted development and death. Similarly, although long-lived marine invertebrate larvae may be exposed to a variety of pathogens during their planktonic period, the toll taken by larval diseases and the role of larval immune responses have not been investigated. Since little information exists concerning the frequency of aborted development and susceptibility of larvae to disease, the relative importance of these factors cannot be compared with other sources of larval mortality.

Recent information concerning the reproductive biology and larval ecology of benthic marine invertebrates has made it possible to elucidate the relative importance of several factors that influence larval survival. For example, seasonal gametogenesis and synchronization of spawning have been suggested as adaptations to ensure fertilization in several temperate and tropical invertebrates (Pearse, 1975, 1981). Seasonal maturation of gonadal tissues appears to be mediated through the activities of nervous and endocrine systems (Pearse, 1965, 1981; Pearse and Eernisse, 1982;

Pearse and Walker, 1986; Pearse and Beauchamp, 1986; Iliffe and Pearse, 1982). These systems are responsive to proximate factors such as seasonally oscillating temperature, photoperiod, salinity, lunar cycles or the abundance of food (see Giese and Pearse, 1974; Kennedy and Pearse, 1975; Olive, 1980, 1981; Olive and Garwood, 1983). Synchronization of spawning and the chemotactic attraction of spermatozoa to recently spawned ova (Miller, 1973, 1977, 1981, 1982) both serve to increase the probability of fertilization in freely spawning invertebrates with dispersive larvae. However, Pennington (1985) gathered field evidence to suggest that sperm dilution may decrease the frequency of encounters between ova and sperm in the sea urchin, Strongylocentrotus droebachiensis. Nevertheless, aggregation of adults, spawning synchrony and the evolution of elaborate electrical and microstructural blocks against polyspermy (see Austin, 1965) are evidence that the ova of benthic marine invertebrates probably experience a high degree of fertilization success.

Rates of larval feeding and diet can also affect larval survivorship, but the direct effects of food supply have proven difficult to analyze in the field. Laboratory studies have shown that differences in larval survivorship are related to both the quality and quantity of food (Davis and Guillard, 1958; Paulson and Scheltema, 1968; Anger et al., 1981; Fenaux, 1982; Lucas, 1982; Paulay et al., 1985; and numerous others). However, it is difficult to ascertain the relative importance of larval feeding and starvation, particularly in light of recent discoveries concerning the uptake of dissolved organics as a source of larval nutrition (Manahan, 1983; Manahan and Crisp, 1982: Manahan et al., 1983; de Burgh and Burke, 1983; Davis and Stephens, 1984).

The effects of ambient thermal conditions on embryological development and survival have received widespread attention (Kinne, 1970; Pechenik, 1981; Clarke, 1982; Bosch et al., 1984). The thermal conditions under which successful reproduction can occur are typically narrower than the range of adverse temperatures normally tolerated by adults (Mileikovsky, 1960; Scheltema and Williams, 1982). However, temperatures that are detrimental to early embryological stages are generally similar to the ambient extremes encountered by embryos and larvae during the pelagic period (Lonning, 1959; Moore, 1959; Davis and Calabrese, 1964; Calabrese, 1969). Furthermore, Andronikov (1975) demonstrated that thermal tolerance increases substantially in later embryos and larvae from several molluscs and echinoderms. In most cases, natural changes in sea temperature were a limiting factor only during critical early stages of development. The detrimental effects of pollutants and other adverse environmental conditions have also been studied with respect to their influence on the survival of marine invertebrate larvae (Bookhout and Costlow, 1974; Bigford, 1979; Crisp, 1984; Marsh et al., 1986), although the negative effects of sub-optimal habitats are generally thought to be restricted to bodies of water characterized by slow replacement rates such as lagoons, partially enclosed bays, and fjords.

Substratum selection is also an important process influencing the survivorship of marine invertebrate larvae. Obrebski (1979) proposed a simple model to account for differences in adaptations for colonization by settling larvae, and he made the intuitive prediction that traits that reduce larval mortality, such as larval defenses and discriminatory substratum selection, should be favored when conditions for larval survival in the plankton are poor. Nearly all species with dispersive larvae exhibit some degree of substratum selectivity (see reviews by Meadows and Campbell, 1972; Crisp, 1974; Scheltema, 1974; Chia _et al_., 1984). However, studies that examine the relative importance of substratum selection to the survivorship of settling larvae and post-settlement stages are still in their infancy (Connell, 1985; Gaines and Roughgarden, 1985; Young and Chia, in press). Presumably, recognition of specific cues associated with suitable habitats should serve to decrease the loss of larvae due to settlement in a hostile site. Meaningful assessments of the relative importance of pre-settlement and post-settlement events in determining temporal and spatial patterns of larval survivorship and juvenile recruitment constitute a challenge worthy of considerable attention.

Large-scale losses of planktonic larval stages have also been attributed to offshore transport of larval populations into areas that are unsuitable for settlement. Jackson and Strathmann (1981) examined the synergistic interactions between eddy mixing, rates of larval mortality, and the lengths of the precompetent and competent periods of development as factors in their model of larval survivorship. Jackson and Strathmann (1981) concluded that offshore mixing could potentially be as detrimental to larval populations as high rates of predation or the inability of a larva to locate a suitable settlement site. However, Jackson and Strathmann's (1981) predictions are based on the assumption that predators kill larvae at equivalent rates during the precompetent and competent periods. Although some empirical data have been gathered to support this assumption (Rumrill, 1987), in most cases the susceptibility of early larval stages differs substantially from that of later stages (Rumrill _et al._, 1985; Rumrill, 1987). Offshore transport can indirectly influence larval survivorship by: 1) increasing the risk of predation as larvae prolong their planktonic period in the absence of a suitable settlement site, or 2) by the establishment of pseudopopulations composed of non-reproductive individuals (Mileikovsky, 1968; Gage and Tyler, 1981). By comparison, the direct detrimental effects of offshore mixing may be minimal along continental shelf regions where the net advective transport of larvae is along the shore rather than prependicular to the coast.

Although several factors contribute to the mortality of marine invertebrate larvae, it is likely that adverse hydrographic conditions, failure to locate an adequate substratum for settlement, and predation upon larvae are the most significant sources of larval death. Since little empirical data exist to critically examine rates of invertebrate larval mortality, it is premature to estimate whether larval losses due to predation exceed or are surpassed by losses due to offshore transport or the inability of a larva to locate a suitable site for settlement and metamorphosis. These processes have important implications concerning the dynamics of benthic invertebrate populations because the availability of metamorphically competent larvae dictates the intensity and spatial pattern of recruitment events.

D. PRIMARY OBJECTIVES OF THE RESEARCH

In the present study, I develop the thesis that larval mortality is a fundamental component of the contrasting life history traits exhibited by benthic marine invertebrates. In particular, I address the following questions: (1) Are the life history traits of marine invertebrate faunal assemblages influenced by environmental variability on small as well as large geographic scales? (2) Do characteristic patterns of age and stage-specific larval mortality exist in nearshore waters, or are the life tables for planktonic larval populations essentially chaotic? (3) How is the risk of predation during the planktonic period related to initial ova size and the intrinsic rate of development? (4) Can marine invertebrate larvae be considered as "sitting ducks" in predator-prey equations? If not, what types of ontogenetic features function effectively in the defense of larvae against predatory zooplankton? (5) How does mortality during the planktonic period compare with mortality during settlement?

Given the thesis that predation upon larvae is a primary cause of death during the planktonic period, and provided that laboratory studies of predator-prey interactions are appropriate to describe stage-specific differences in survivorship, it should be possible to discover a series of general patterns of larval susceptibility.

E. APPLICABILITY OF ECHINODERM EMBRYOS AND LARVAE

The extant Echinodermata are representative of an ancient phylum of deuterostomate metazoans that first appeared in the fossil record during the lower Cambrian (Sepkoski, 1981). The phanerozoic history of the echinoderms, like that of several other groups of benthic marine invertebrates, has been one of diversification followed by periods of decline and rediversification (Valentine, 1973; Valentine and Jablonski, 1983; Raup, 1979; Sepkoski, 1981). Early echinoderms underwent an initial period of diversification during the Ordovician, and during their apex in the Silurian the phylum was represented by over 25 classes. The diversity of echinoderms declined drastically during the Permian-Triassic extinctions, followed by a second period of diversification in the middle Jurassic. These periods of Paleozoic and post-Paleozoic diversification provided a historical testing ground for the success of novel body plans. Comparisons of modern and fossil assemblages indicate that the Recent echinoderm fauna is largely representative of species that inhabited shallow continental seas during the late Jurassic and Cretaceous periods (Fell, 1966; Blake, 1982; Smith, 1984).

Interest in the origins and evolution of echinoderms has led to the inference that the ancestral larval form was pelagic and planktotrophic (Jagersten, 1972; Strathmann, 1978). The ancestral planktotrophic larval form has presumably been lost from the Crinoidea, and the published literature suggest that the extant crinoids may be entirely lecithotrophic (Mortensen, 1920; Dan and Dan, 1941; Hyman, 1955; Strathmann, 1978; Mladenov and Chia, 1983; Chia _et al_., 1986). In contrast, the other principal echinoderm clades (Asteroidea, Ophiuroidea, Echinodiea, and Holothuroidea) have retained a greater degree of developmental flexibility. Members of these groups exhibit planktotrophic, lecithotrophic, and vivparous modes of development (Chia, 1966; Hendler, 1975; Rumrill, 1982; McEuen, 1986; Emlet et al., 1986). The larval stages of Recent echinoderms provide an opportunity to study the ecological consequences associated with divergent reproductive traits, and to address questions concerning the evolution of complex life cycles.

The approach of studying intraspecific and interspecific variability of larval susceptibility among echinoderm embryos and larvae has inherent advantages and disadvantages. Advantages offered by this phylum include: 1) widespread ecological interest in the rates of development, feeding biology and survivorship of larval echinoderms, 2) a diversity of larval body forms and trophic modes, 3) considerable published information about the breeding periods and modes of development for local species, 4) convenience of rearing large numbers of sibling larvae under controlled laboratory conditions, and 5) the existance of a body of literature spanning over a century that identifies laboratory techniques for manipulations of larval morphology, size and behavior. Disadvantages associated with conducting the research with echinoderms include: 1) restrictions on the types of swimming behavior exhibited by larvae, 2) seasonal breeding periods that prohibit direct comparisons of the effects of seasonally abundant predators, and 3) relatively long-lived larvae that require considerable laboratory attention.

F. ORGANIZATION OF THE THESIS

The central theme of this research is an examination of patterns and processes that contribute to predator-induced mortality of echinoderm embryos and larvae. The thesis is written in the form of 5 papers, each dealing with different aspects of echinoderm larval mortality. The research topics were selected from Thorson's (1950) plenary catalog of factors that influence rates of larval mortality. As a consequence of their similar theme, the thesis chapters overlap partially in their reference to published literature and in their discussion of the implications of differential larval susceptibility. I have made a conscious effort to keep the redundancy to a minimum. Each paper is written in the format required by the journal to which it has been or will be submitted for publication.

In the first appendix of the thesis, I describe small-scale biogeographic variation in the diversity of life history traits among 37 species of echinoderms from a variety of habitats within Barkley Sound, British Columbia. The survey provides comparative information about the diversity, abundance, and life history traits of echinoderms along an environmental gradient ranging from protected mudflats to exposed rocky intertidal and subtidal habitats. In addition, I compare factors that contribute to small and large-scale biogeographic patterns in the distribution of planktotrophic, lecithotrophic and brooding species among echinoderm faunal assemblages located along the north-east Pacific coast.

Chapter Two documents stage-specific differences in the susceptibility of sand dollar embryos and larvae to predation by a carnivorous microcrustacean. Losses of larvae to predators are examined in a series of laboratory microcosm feeding experiments to allow for the recognition of larval susceptibility patterns in single and mixed-stage feeding experiments. I describe a post-contact predator avoidance response in echinopluteus larvae, and I draw speculative conclusions about the importance of high rates of early mortality in estimating the losses of larvae due to predation in nearshore waters.

In Chapter Three, I examine the effects of development rate on the cumulative risk of predation during the planktonic period for 3 species of sea urchins and 4 species of sea stars. Interspecific differences in ova volume and temperature-dependent changes in development rate are utilized to compare the effects of accelerated and retarded differentiation on predation by carnivorous microcrustaceans.

Hydromechanical aspects of locomotion and prey capture are analyzed for raptorial zoea larvae of a decapod crustacean in Chapter Four. I utilize stroboscopic photography and flow-visualization techniques to describe the mechanics of swimming and prey capture. My results indicate that swimming velocities fluctuate markedly over short periods of time, and that unsteady aspects of locomotion (acceleration and deceleration) can be an important component of predation upon non-motile embryos and ciliated echinoderm larvae.

In the Fifth Chapter, a post-facto approach is developed to assess the relative importance of pre-settlement and post-settlement factors that influence patterns of echinoderm recruitment. A spatially heterogeneous pattern of recruitment between adjacent populations of an asterinid sea star, *Asterina miniata* (Brandt, 1835) is described, and I present empirical laboratory and field data to address several alternative hypotheses that may be invoked to explain the observed pattern of recruitment. Experimental evidence suggests that larval substratum selectivity and differences in the abundance and spatial distribuion of benthic suspension feeders can be key determinants of success or failure of *A. miniata* larvae during settlement.

The Sixth Chapter describes the results of a broad survey of echinoderm embryo and larval susceptibility patterns. Results from the survey allow for the recognition of predator functional groups. In addition, I describe five different patterns of differential susceptibility. The Type A pattern (high susceptibility of embryos and early larvae) appears frequently within the matrix and may be typical of mortality patterns in the field.

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CHAPTER II.

DIFFERENTIAL SUSCEPTIBILITY OF MARINE INVERTEBRATE LARVAE: PREDATION UPON *Dendraster excentricus* (ECHINOIDEA: CLYPEASTEROIDA) EMBRYOS AND LARVAE BY ZOEAE OF THE RED ROCK CRAB *Cancer productus* (CRUSTACEA: DECAPODA) [1]

A. INTRODUCTION

Recent life history models consider rates of larval mortality as pivotal points in the evolution of reproductive traits in benthic marine invertebrates. In general, the energetic costs and reproductive benefits associated with planktotrophic, lecithotrophic and brooding modes of development are compared intuitively, and mathematical solutions are derived that minimize the cost and benefit ratio (Vance, 1973; Chia, 1974; Strathmann, 1977; Grant, 1983). Although this approach provides valuable insight for contrasting life history patterns among benthic invertebrates, it is not entirely satisfying because estimates of relative cost must take into account energetic expenditure and larval survivorship.

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[1] A version of this chapter has been published. Rumrill, S. S., Pennington, and F. S. Chia. 1985. Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz) embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. J. exp. mar. biol. Ecol. 90: 193-208.

Planktonic embryos and larvae are preyed upon by a variety of predators including carnivorous zooplankton, planktivorous fish, benthic invertebrates and protozoans (Lebour, 1922, 1923; Korringa, 1941; Thorson, 1946; Barnes, 1959; Yamaguchi, 1973; Mileikovsky, 1974; Sebens and Koehl, 1984; Young and Chia, in press). Despite the potential importance of predation to larval survival, little is known of the interactions that occur between predators and their invertebrate larval prey. The susceptibility of embryos and larvae to capture may change during ontogeny due to: 1) predator size-selection (Landry, 1978), 2) stage-dependent differences in prey distribution (Omori and Hamner, 1982; Yen, 1982), and 3) developmental changes in prey morphology and behavior (Pennington and Chia, 1984). As a consequence, discriminatory prey selection and differential larval susceptibility may apply selective pressures on the larval phase of invertebrate life histories favoring traits that reduce predator-induced mortality.

The sand dollar, Dendraster excentricus, is a common member of sandy intertidal and subtidal communities along the Pacific coast of North America (Merrill and Hobson, 1970; Birkeland and Chia, 1971). Individuals of D. excentricus spawn from March-June (Mortensen, 1921; Niesen, 1977) and the embryos develop into feeding larvae that have a planktonic period lasting from 5-6 wk (Highsmith, 1982). Throughout the planktonic period embryos and larvae of D. excentricus are exposed to risk from a variety of potential predators that include the mussel, *Mytilus edulis* and the solitary ascidian, *Styela gibbsii* (Cowden *et al*., 1984) as well as several species of carnivorous zooplankton (Pennington *et al*., 1986). Timko (1979) reported that adult sand dollars from southern California preyed upon conspecific larvae in laboratory cultures; larviphagy, however, could not be demonstrated in *D. excentricus* from Puget Sound (Chia and Atwood, 1982). Benthic tanaid crustaceans (*Leptochelia dubia*) prey upon recently metamorphosed *D. excentricus* (Highsmith, 1982), and *L. dubia* and epibenthic amphipods also capture settling *D. excentricus* plutei (Rumrill, personal observations).

In this study I describe predator-prey interactions between various developmental stages of *Dendraster excentricus* (Eschscholtz) and zoea larvae of the red rock crab, *Cancer productus* Randall. Decapod zoeae were chosen as predators because they often occur in dense aggregations in nearshore waters and are suspected to be important predators of larvae and other small zooplankton (Sulkin, 1974, 1978, 1984; Sulkin and Van Heukelem, 1980; Incze and Paul, 1983). Although *C. productus* zoeae and *D. excentricus* larvae may not always interact in temperate nearshore waters, *C. productus* are representative of carnivorous microcrustaceans that co-occur with planktonic larvae of *D. excentricus*. Laboratory observations demonstrate stage-dependent susceptibility of *D. excentricus* embryos and larvae to capture by *C. productus* zoeae. The ability of

D. excentricus plutei to reverse the direction of swimming is identified as a post-contact encounter response that reduces rates of larval mortality.

B. MATERIALS AND METHODS

The research was carried out from April-June 1983 at the Friday Harbor Laboratories, Washington (48° 32'N, 123° 05'W), and from June-August, 1983, at Bamfield Marine Station, British Columbia (48° 50'N, 125° 08'W).

1. Larval Abundance

Distribution patterns of echinoid larvae and brachyuran zoeae were determined in Barkley Sound, British Columbia, from a series of vertically stratified zooplankton tows taken at three depth strata with 125 μm mesh, 0.5 m diameter standard and closing nets. Three replicate samples were taken between depths of 0-30 m, 30-60 m, and 60-90 m. All plankton tows were taken on 15 July 1983, between 0930 and 1015 hrs. Each tow was preserved in 10% buffered formalin immediately after collection and sorted under a Wild M5A stereomicroscope. Dendraster excentricus larvae were examined with cross-polarized light and identified on the basis of skeletal characteristics (Strathmann, 1979). Cancer productus zoeae were identified using keys provided by Trask (1970) and Hart (1971).

2. Functional Response of Cancer predation

Fifth zoea stage Cancer productus were selected as predators for the feeding experiments because they were the most abundant zoea instar in the surface waters. Individuals of _C_. _productus_ were collected in hand-held jars and maintained in the laboratory in running unfiltered seawater aquaria for 3-5 days before they were used in experiments. Carapace diameters of zoeae averaged 1.7 mm and the mean rostrum-dorsal spine length was 4.6 mm. Prey stages of _Dendraster_ _excentricus_ were obtained by inducing adults to spawn with intracoelomic injections of 0.52 M KCl. Echinopluteus larvae of _D_. _excentricus_ were cultured at 12°C in 3.7 liter glass bottles containing 1 µm filtered seawater. Echinoplutei were fed a 2:1 mixture of _Dunaliella_ _tertiolecta_ Butch. (Chlorophyta) and _Pavlova_ _lutheri_ Droop (Chrysophyta) every 2-3 days when the seawater was replaced.

The effects of prey density on _Cancer_ _productus_ predation rates were determined in laboratory feeding experiments. In each trial, _Dendraster_ _excentricus_ embryos were counted into 1 liter glass jars filled with 1 µm filtered seawater. At the initiation of each experiment five _C_. _productus_ zoeae were added to each jar. No zoeae were added to control jars. Each trial consisted of three replicate predator treatments and two controls. Separate experiments were conducted with _D_. _excentricus_ embryos at concentrations of 25, 50, 100, 250, and 500 prey l^{-1}. The jars were strapped horizontally around the long axis of a cylindrical mixing device (see Yen, 1982) that rotated at 1.7 rpm to keep the predators and prey suspended. All feeding experiments were conducted in a cold room or incubator at 12°C with 12L:12D photoperiod. After 24 hrs the remaining larvae were counted and C. productus clearance rates were calculated as:

$$C = (V / t)(\ln D_1 - \ln D_2)$$

where C is the clearance rate in liters $\text{zoea}^{-1}\ \text{day}^{-1}$, V is the volume of seawater available per zoea, t is the duration of the experiment, and D_1 and D_2 are the initial and final densities of prey (Vanderploeg and Scavia, 1979).

3. Differential Susceptibility of Embryos and Larvae

The relative susceptibility of Dendraster excentricus embryos and larvae to predation was determined by conducting feeding experiments with seven different ontogenetic stages of prey (see Table 1). The prey categories were : 1)ova surrounded by intact jelly coatings and pigment cells, 2) ova without jelly coatings and pigment cells, 3) embryos through gastrula stages, 4) prism larvae, 5) 4-armed plutei, 6) 6-armed plutei, and 7) 8-armed plutei. Prey items for category no. 2 were prepared by passing fully hydrated D. excentricus ova through 125 um mesh. Prey stages in category # 3 were non-motile embryos at the beginning of the experiment but had developed into swimming gastrulae when the experiments were terminated.

Differential prey susceptibility was examined

Table 1

Categories of *Dendraster excentricus* prey used in feeding experiments and their characteristic shapes, sizes and motility: Table entries are means; n = 25 measurements per category; (a) diameter; (b) greatest length; (c) greatest width X greatest length.

PREY CATEGORY	SHAPE	SIZE (μm)	MOTILITY
1. Ova with jelly coats	Spherical	155 (a)	Non-motile
2. Ova without jelly coats	Spherical	121 (b)	Non-motile
3. Embryos - Gastrulae	Prolate Sphere	121 - 142 (b)	Forward Swimming
4. Prism Larvae	Pyramidal	115 X 132 (c)	Forward Swimming
5. 4-armed Pluteus	Elongate Pyramid	328 X 284 (c)	Forward + Reverse Swimming
6. 6-armed Pluteus	Elongate Pyramid	479 X 654 (c)	Forward + Reverse Swimming
7. 8-armed Pluteus	Elongate Pyramid	504 X 716 (c)	Forward + Reverse Swimming

independently by simultaneously offering several different stages of *Dendraster excentricus* to *Cancer productus* zoeae. Two series of mixed stage feeding experiments were conducted. In the first set, 20 embryos, 20 prism larvae and 20 6-armed plutei were placed into a 2 liter separating funnel containing 5 zoeae. In the second set 20 gastrulae, 20 4-armed plutei and 20 8-armed plutei were added to the funnel along with 5 zoeae. The initial density of prey in both sets of experiments was 30 *D. excentricus* liter^{-1}. Each set of experiments consisted of three replicate treatments with *C. productus* zoeae and two controls without zoeae. Filtered seawater in the funnel was maintained at 12-13^{o}C by a jacket of circulating seawater, and a stream of small air bubbles (5-8 min^{-1}) kept the predators and prey suspended. After 24 hrs the number of *D. excentricus* remaining was determined for each prey category.

The effectiveness of several potential prey defenses was investigated by conducting feeding experiments with variously treated prey. First, increasing prey size was evaluated by comparing rates of predation upon normal and dwarf-sized 4-armed plutei. Dwarf plutei were obtained by culturing blastomeres that had been physically separated following the second cell division. Dwarf plutei were similar in form and behavior to normal plutei, and nearly equivalent in size to gastrulae and prism larvae cultured from non-dissociated blastomeres. Second, the effects of prey visibility were examined by conducting feeding experiments under conditions of constant illumination and darkness. Predation experiments were also conducted with dyed prey under constant illumination. Four-armed plutei were dyed crimson by immersing them for 10 min in seawater containing 0.01% Neutral Red. Dyed plutei remained active and swam normally for up to 72 hrs following the dye treatment. Third, the effects of prey motility were assessed by comparing rates of predation upon swimming and non-swimming plutei. Four-armed plutei were immobilized by heating them to 40°C for 60 s. Finally, the importance of periodic reversals in the direction of swimming was evaluated by comparing rates of predation upon normal plutei and plutei whose capability for ciliary reversal had been blocked by 0.01% $MgCl_2$ (Mackie _et_ _al_., 1969; Strathmann, 1971). The $MgCl_2$ appeared to have a negligible effect on the swimming and feeding of _Cancer productus_ zoeae but inhibited ciliary reversal and backwards swimming in _Dendraster excentricus_ plutei. All experiments with treated prey were conducted for 24 hrs at initial densities of 50 prey $liter^{-1}$ and consisted of three replicate predator treatments and two controls without predators.

4. _Post-Contact Encounter Response_

To analyze the swimming behavior of different prey stages of _Dendraster excentricus_ during encounters with _Cancer productus_ zoeae, I placed _D. excentricus_ gastrulae and 4-armed plutei together with zoeae in a glass observation chamber (6 X 2 cm) containing 1 µm filtered seawater. The observation chamber was illuminated with transmitted diffuse light and cooled to ambient sea temperature with a circulating bath. Swimming movements of the zoeae were restricted by tethering their dorsal spines to glass capillary tubes filled with plasticene. The tethered zoeae continued to beat their maxillipeds and create ventrally-directed feeding currents in the observation chamber for periods lasting up to 8 days. The direction and velocity of feeding currents near the carapace of the tethered zoeae ranged from 5.9 to 8.6 mm s^{-1} and were nearly identical to the direction and velocity of currents generated during normal swimming (see Rumrill, 1987). An outline of a tethered zoea was traced with a camera lucida to provide a reference for plotting predator-prey encounters. The slow swimming speeds of larval D. excentricus (0.94 mm s^{-1}) made it possible to visually record encounters between prey and the stationary C. productus zoeae. Stage-specific capture frequencies were calculated as the proportion of attacks resulting in capture and ingestion.

C. RESULTS

1. Larval Abundance Patterns

Echinoid larvae and brachyuran zoeae were both concentrated in surface waters and showed distribution patterns that were significantly different from uniform

(Table 2, Kruskal-Wallis ANOVA, $p < 0.05$). *Cancer productus* zoeae were more abundant than *Dendraster excentricus* in plankton tows collected from 0-30 m, but low numbers of both *C. productus* and *D. excentricus* occurred in water deeper than 30 m. Total numbers of larvae were highly variable between successive tows and provide an indication that predator and prey populations had patchy spatial distributions. Dense aggregations of *C. productus* zoeae and megalopae commonly occur in the upper surface waters where they have been observed by submersible and SCUBA divers (Rumrill, pers. observations).

2. *Functional Response of Cancer Predation*

The ingestion rate by *Cancer productus* zoeae increased in a curvilinear manner with increasing initial prey abundance (Figure 1a, $t = 6.35$, $p < 0.001$). The mean (± s.d.) ingestion rate was 11.05 ± 8.52 embryos zoea^{-1} day-1 for initial *Dendraster excentricus* densities between 25 and 500 prey l^{-1}. In contrast, clearance rates by *C. productus* zoeae generally declined with increasing initial prey density and showed a Holling (1966) Type II functional response curve (Figure 1b). The increase in *C. productus* foraging effort in response to low prey availability indicates that the rate of embryo capture is directly related to the frequency of encounters between zoeae and *D. excentricus* embryos in feeding vessels.

3. *Differential Susceptibility of Embryos and Larvae*

Clearance rates by *Cancer productus* zoeae upon various

Table 2

Vertical abundance of echinoid larvae and brachyuran crab zoeae by depth stratum in Barkley Sound, British Columbia: Values shown are mean ± s.d.; values in parentheses indicate numbers of Dendraster excentricus and Cancer productus larvae. The results of Kruskal-Wallis ANOVA tests of the depth stratification of larvae are also shown along with their associated probability values.

DEPTH STRATUM m	NUMBER TOWS	SAMPLE VOLUME m^3	PLUTEI # m^{-3}	ZOEAE # m^{-3}
0 - 30	3	11.8 ± 2.9	136 ± 62 (12 ± 6)	515 ± 292 (47 ± 30)
30 - 60	3	11.7 ± 2.0	44 ± 46 (3 ± 3)	37 ± 14 (3 ± 1)
60 - 90	3	12.3 ± 3.1	0	10 ± 8 (1 ± 1)

Kruskal-Wallis ANOVA (stratification by depth)

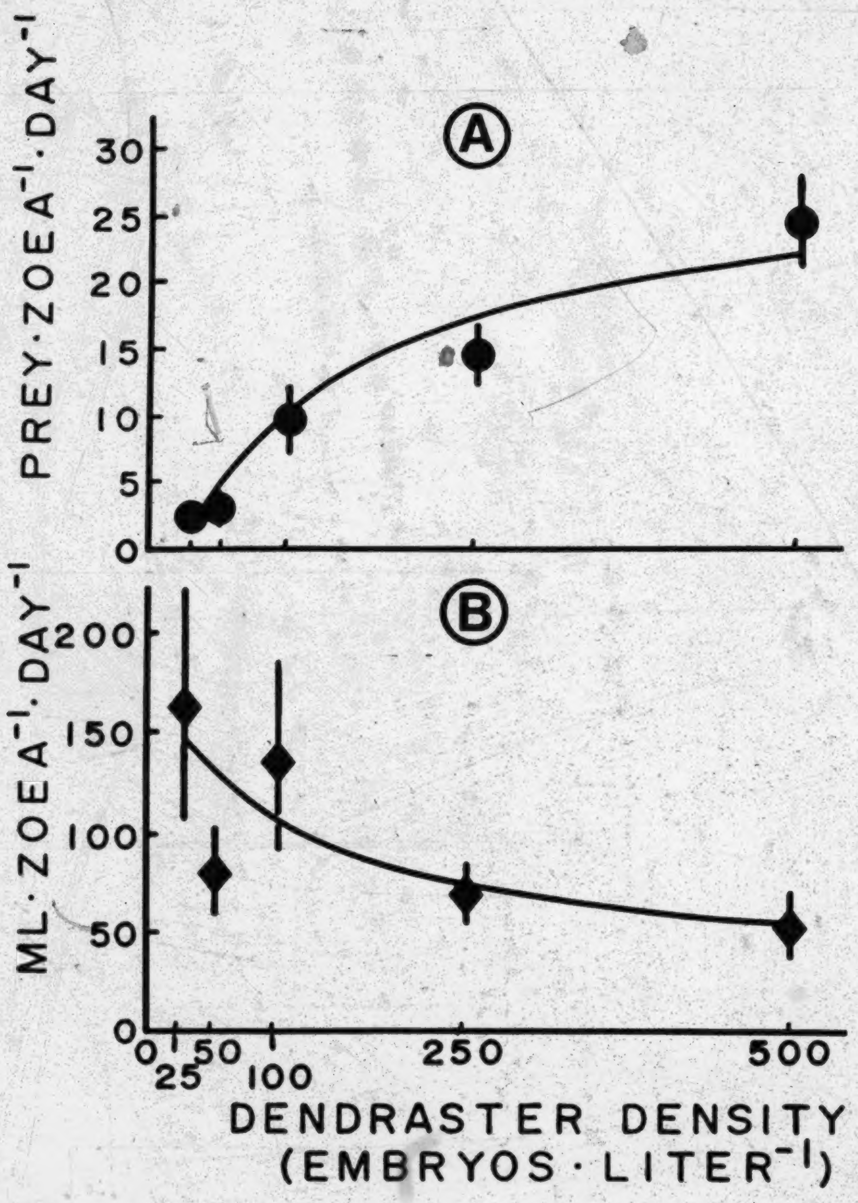
All echinoplutei H = 7.2099 $p = 0.0272$

Dendraster excentricus H = 7.7968 $p = 0.0203$

All brachyuran zoeae H = 7.2000 $p = 0.0273$

Cancer productus H = 7.1813 $p = 0.0275$

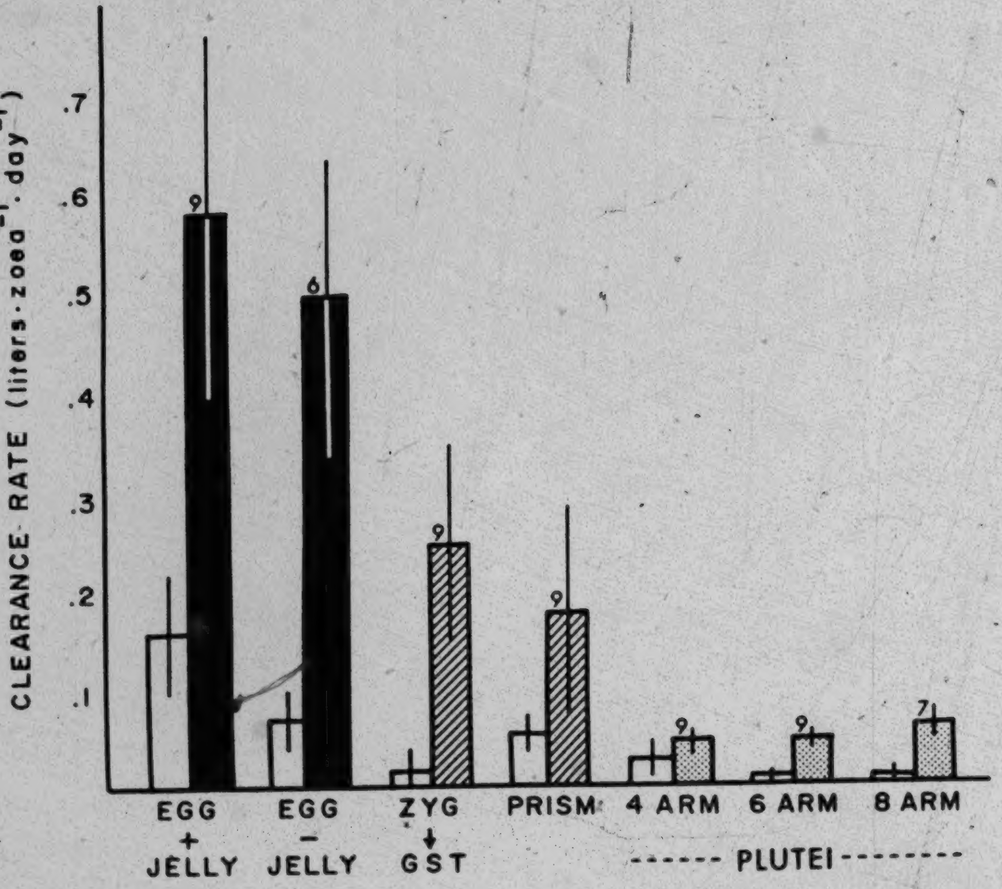
Figure 1. Functional response of Cancer productus predation to abundance of Dendraster excentricus embryos. Values shown are means ± s.d. A. Ingestion Rate. Regression curve has the equation $Y = -23.04 + 7.6 \ln X$; $r^2 = 0.90$. B. Clearance Rate. Regression curve has the equation $Y = 242.61 - 29.93 \ln X$; $r^2 = 0.41$.


A
PREY · ZOEA^{-1} · DAY^{-1}
30
25
20
15
10
5
0
B
ML · ZOEA^{-1} · DAY^{-1}
200
150
100
50
0
0
25
50
100
250
500
DENDRASTER DENSITY
(EMBRYOS · LITER^{-1})

developmental stages of Dendraster excentricus are shown in Figure 2. Ova (with and without jelly coatings) were captured at a high rate (pooled mean = 0.55 ± 0.17 liters $zoea^{-1}$ day^{-1}, n = 15) while gastrulae and prism larvae were captured at an intermediate rate (pooled mean = 0.22 ± 0.11 liters $zoea^{-1}$ day^{-1}, n=18). Low clearance rates were observed for pluteus larvae that had 4, 6 or 8 arms (pooled mean = 0.05 ± 0.02 liters $zoea^{-1}$ day^{-1}, n = 25). Clearance rates differed significantly between the high, intermediate and low susceptibility groups (ANOVA, $p<0.001$). In all cases losses of prey in the feeding trials were significantly greater than incidental losses in controls. Differences in clearance rates were consistently low between the various prey categories; there were no significant differences ($p > 0.05$) between ova with and without jelly coatings (two-sample t-test, t = 0.7826, n.s.), between gastrulae and prism larvae (t = 1.4233, n.s.), nor between pluteus larvae having various numbers of arms (4 vs. 6 arms, t = 0.2147, n.s.; 6 vs 8 arms, t = 1.5119, n.s.; 4 vs. 8 arms, t = 1.5729, n.s.).

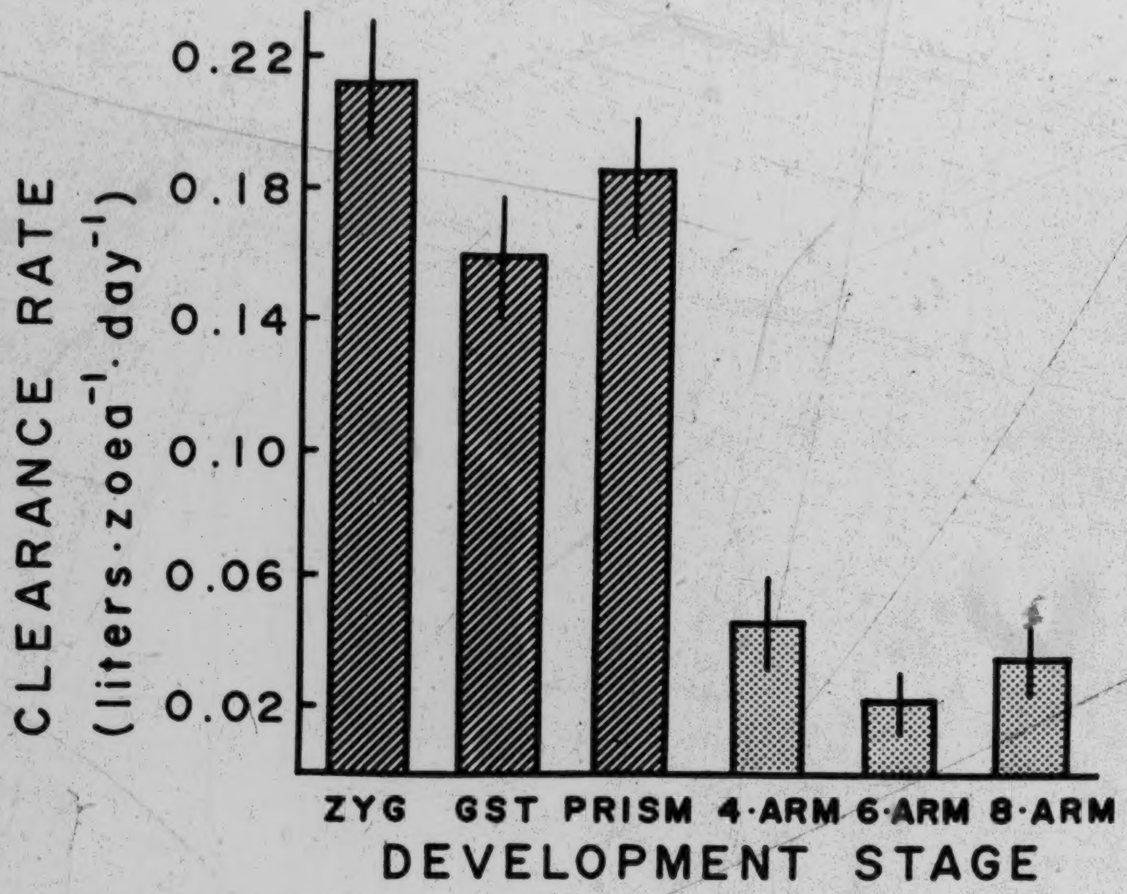
High clearance rates were also observed for embryos, gastrulae and prism larvae when Cancer productus zoeae were offered mixed stages of prey in 2 liter vessels (Figure 3). Clearance rates of C. productus averaged 0.18 liters $zoea^{-1}$ day^{-1} for pre-pluteus stages and 0.03 liters $zoea^{-1}$ day^{-1} for pluteus larvae. Decreased susceptibility of pluteus larvae to predation (Figures 2

Figure 2. Clearance rates by Cancer productus zoeae upon various developmental stages of Dendraster excentricus during single-stage feeding experiments. Solid bars = high vulnerability eggs; hatched bars = intermediate vulnerability zygotes, gastrulae and prism larvae; stippled bars = low vulnerability echinoplutei; Open bars = loss of prey in controls. All values shown are means ± s.d.



Predation of Dendraster by Cancer zoea

Figure 3. Clearance rates by Cancer productus zoeae upon various developmental stages of Dendraster excentricus during mixed-stage feeding experiments. Hatched bars = intermediate vulnerability zygotes, gastrulae and prism larvae; stippled bars = low vulnerability echinoplutei. All values shown are means ± s.d.


CLEARANCE RATE
(liters · zoea^{-1} · day^{-1})
0.22
0.18
0.14
0.10
0.06
0.02
ZYG
GST
PRISM
4·ARM
6·ARM
8·ARM
DEVELOPMENT STAGE

and 3) suggests that stage selective feeding by C. productus or the developmental features associated with the transition of prism larvae into plutei may function to reduce rates of C. productus predation.

Table 3 shows the results of feeding experiments conducted to distinguish among factors that may have contributed to the decreased susceptibility of 4-armed Dendraster excentricus plutei. Differences in prey visibility did not alter the susceptibility of D. excentricus to capture by Cancer productus; clearance rates in experiments carried out in complete darkness and in illuminated conditions with dyed prey were not significantly different from experiments conducted with untreated plutei in the light (Table 3). Feeding experiments conducted with dwarf-sized plutei indicate that susceptibility was independent of absolute body size. Clearance rates during feeding upon dwarf-sized and normal D. excentricus plutei were nearly identical (Table 3) despite the significantly smaller postoral arm lengths of dwarf plutei ($\bar{X}$ = 183.11 ± 41.19 µm) compared with normal plutei ($\bar{X}$ = 388.90 ± 48.46 µm, t = 22.8806, p<0.001). Additional feeding experiments indicated that the motility of D. excentricus had a substantial effect on clearance rates by C. productus. Non-motile heat-killed plutei were captured at significantly greater rates than swimming plutei (Table 3, p = 0.0012). Predation rates upon non-motile plutei were comparable with the intermediate

Table 3

Summary of clearance rates during predation upon variously treated _Dendraster excentricus_ plutei by _Cancer productus_ zoeae. Table entries indicate mean ± s.d. The results of t-test comparisons with feeding experiments conducted with normal-sized plutei in constant light are indicated under the Comparison column. Probability values greater than 0.05 are considered as not significant (n.s.) in the text.

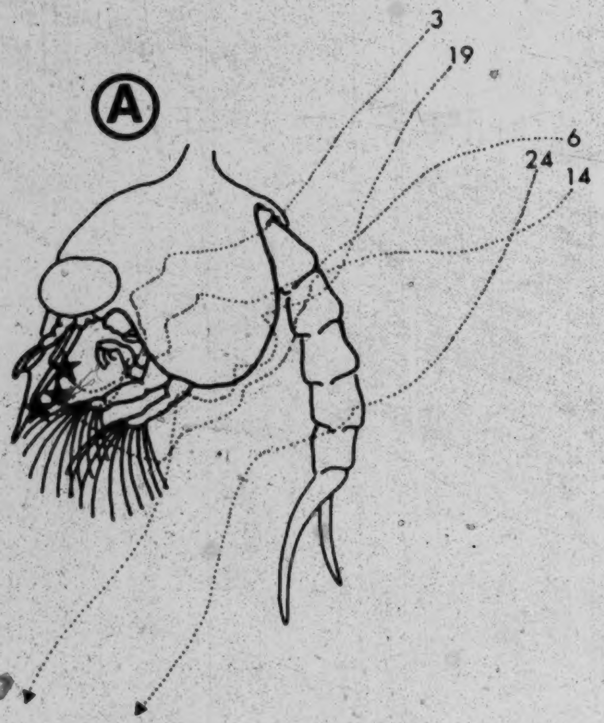
TREATMENT	N	CLEARANCE RATE (ml $zoea^{-1}day^{-1}$)	COMPARISON t	p
Constant Light	5	41.9 ± 18.2	---	---
Constant Dark	6	39.3 ± 12.4	0.6658	0.5206
Dyed Plutei	6	47.9 ± 18.8	0.3631	0.7241
Dwarf-Size Plutei	5	41.5 ± 15.8	0.0291	0.975
Heat-Killed Plutei	6	109.7 ± 24.4	4.6265	0.0012
Anaesthetized Plutei	8	87.5 ± 32.9	2.6865	0.0212

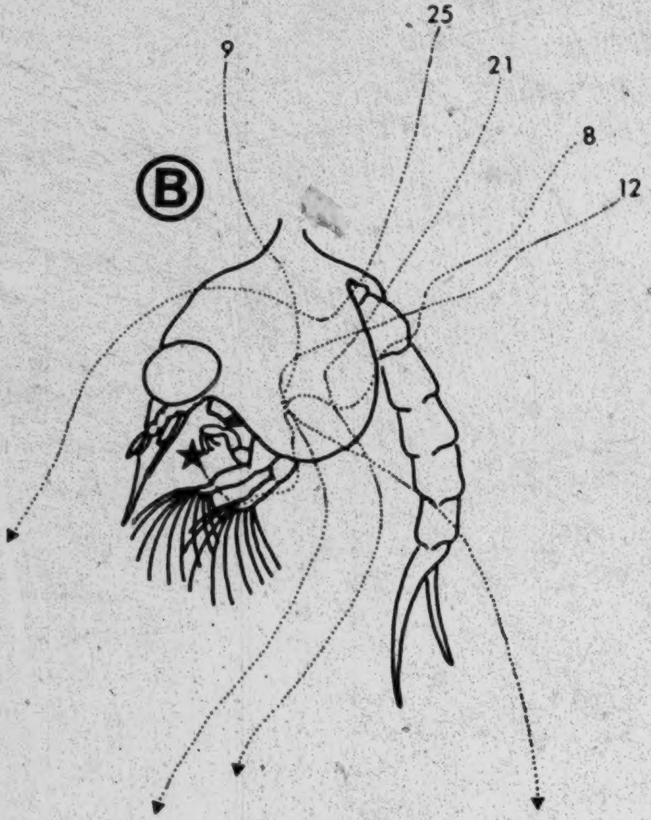
clearance rates observed for earlier stage D. excentricus prism larvae (Figure 2). Increased clearance rates were also observed for plutei whose ability to reverse the direction of ciliary beating was blocked with 0.01% $MgCl_2$ (Table 3, p = 0.0212). Plutei of D. excentricus develop the ability to reverse the direction of swimming during the transition from prism to pluteus. Since $MgCl_2$-treated plutei were incapable of reversed swimming, the high predation rates observed in treatments in which reversal was inhibited indicate that the ability of plutei to reverse the direction of swimming can have a direct effect on the probability of capture by C. productus zoeae.

4. Post-Contact Encounter Response

Interactions between Dendraster excentricus and Cancer productus are shown graphically in Figure 4. Gastrulae and pluteus larvae of D. excentricus made initial contact with the zoea near the postero-dorsal region of the zoea carapace and abdomen due to the flow of ventrally-directed swimming currents generated by the 1st and 2nd maxillipeds. Following the initial contact, D. excentricus gastrulae continued to swim forward and made repeated contact with the zoea carapace, maxillipeds and maxillary setae (Figure 4a). In most cases, gastrulae made repeated contact with the zoea prior to capture. Plutei of D. excentricus also approached the postero-dorsal region of the zoea carapace while swimming forward (Figure 4b), but following the initial contact most plutei immediately reversed the

Figure 4. Camera lucida tracings of encounters between *Dendraster excentricus* gastrulae and echinoplutei and tethered *Cancer productus* zoeae. A. Gastrulae. B. Echinoplutei. Each drawing was prepared by selecting five tracings at random from a set of 25 encounter tracings. Values indicate tracing number; arrows show the direction of prey movement; stars indicate capture and ingestion.


A


B

direction of swimming and moved away from the tethered zoea. Plutei resumed forward swimming when they were 2-3 mm away from the zoea. Plutei of D. excentricus were captured in 12% of the encounters compared with a 56% capture frequency for gastrulae. These observations provide direct evidence that the development of reversed swimming reduces the susceptibility of pluteus larvae to capture by C. productus zoeae in the laboratory.

D. DISCUSSION

Results from this study demonstrate that Cancer productus zoeae are able to capture embryos and early larval stages of Dendraster excentricus at a high rate compared with capture rates for older pluteus larvae. Clearance rates by C. productus zoeae were consistently lower in single and mixed-stage feeding experiments after D. excentricus had developed skeletal elements and the ability to reverse the direction of swimming. The high susceptibility of non-motile stages such as ova and pre-hatched embryos suggests that D. excentricus may be at the greatest risk to planktonic predators immediately after spawning. Factors that may influence the decreased susceptibility of D. excentricus plutei to predation include: 1) size-selectivity, 2) larval morphology, 3) motility, and 4) behavioral responses.

1. Size-Selective Predation

One explanation for the observed pattern of differential susceptibility to predation is that *Cancer productus* zoeae may prefer small ova and embryos over larger plutei. Size-selective feeding has been reported for several freshwater and marine zooplanktonic crustaceans (Dodson, 1974; Kerfoot, 1977; Landry, 1978; Mullin, 1979; Zaret, 1980; Murtaugh, 1981; Pastorok, 1981; Yen, 1982; Landry *et al*., 1985) in which the predators typically have a greater selective impact on small and intermediate-sized prey. Similarly, early stage decapod zoeae are generally limited in the sizes of prey they can consume (Costlow and Bookhout, 1959; Rust and Carlson, 1960; Sulkin, 1975). Prey selection, however, appears to be related both to the size and stage of the zoea as well as the size and nutritional content of the prey (Sulkin, 1978; Levine and Sulkin, 1984). Later stage zoea from several species of crabs including *C. productus* have been reared on diets composed of rotifers, polychaete trochophores, sea urchin gastrulae, and brine shrimp nauplii (Costlow and Bookhout, 1959; Rust and Carlson, 1960; Costlow *et al*., 1966; Poole, 1966; Herrnkind, 1968; Reed, 1969; Trask, 1970; Rice and Williamson, 1971; Sulkin, 1975; Christiansen and Yang, 1976). All of these prey items have body lengths ranging from 70 to 350 µm. I observed predation by *C. productus* upon barnacle nauplii (*Pollicipes polymerus*) and *Dendraster excentricus* plutei that had body lengths greater than 500 µm (Rumrill, personal observations). The 5th instar *C. productus* zoeae were able to capture and ingest all sizes of prey offered in the feeding experiments. Low clearance rates observed during predation upon dwarf-sized D. excentricus plutei suggest that the reduced susceptibility of pluteus larvae is not solely due to increasing prey size. Consequently, explanations other than size-selection must be considered.

2. Larval Morphology

A second possibility for differential prey susceptibility is that later developmental stages of Dendraster excentricus may require longer handling times than earlier stages prior to ingestion by Cancer productus. Growth of post-prism D. excentricus larvae is accompanied by the development of a rigid internal skeleton and a band of cilia that extends around the periphery of the larval arms (Burke, 1983). Handling times of D. excentricus may increase following the development of the skeleton, and could result in a decreased average ingestion rate for later prey stages. However, significantly higher capture rates were observed for heat-killed plutei compared with normal plutei, despite the presence of skeletal ossicles and long postero-lateral and postoral arms in live and heat-killed prey. Emlet (1982) noted that echinoplutei of D. excentricus have fenestrated skeletal spicules and are capable of flaring the postero-lateral arms when disturbed. Arm flaring temporarily increases the width of the pluteus, and Emlet (1983) suggested that fenestrated arms and flaring behavior may deter predation. Although experiments have not been conducted that specifically address arm-flaring, results from this study indicate that the development of a rigid skeleton is not entirely effective in eliminating predation. Analysis of *C. productus* gut contents with cross-polarized light immediately following feeding experiments revealed crushed sections of fenestrated spicules along with other tissues from ingested *D. excentricus* plutei. No differences in prey susceptibility could be detected between *D. excentricus* and other echinoplutei (*Strongylocentrotus franciscanus* and *S. purpuratus*) that have non-fenestrated skeletons and are incapable of flaring behavior (Rumrill and Chia, 1985). However, the possibility that arm flaring and skeletal morphology may reduce predation rates by increasing the handling times of plutei prior to ingestion cannot be excluded.

3. *Dendraster Motility*

The encounter model developed by Gerritsen and Strickler (1977) predicts that increasing prey swimming speed will increase the probability of encounters between predators and prey. The slow swimming speed of *Dendraster excentricus* and low densities of *Cancer productus* zoeae in Barkley Sound indicate that ontogenetic differences in the swimming speed of *D. excentricus* will have a negligible effect on encounter rates with *C. productus* in nature. For example, the maximum density of *C. productus* observed in Barkley Sound was 73 zoeae m^{-3}. Assuming random distributions of predators and prey, non-motile D. excentricus embryos should encounter C. productus zoeae once every 29 hrs compared with an encounter interval of 28 hrs for swimming D. excentricus plutei. Encounter rates with C. productus zoeae were also similar between non-motile (2.31 zoeae embryo^{-1} hr^{-1}) and motile prey stages (2.32 zoeae pluteus^{-1} hr^{-1}) at the elevated predator and prey densities in laboratory experiments. Despite these small differences in encounter frequencies, the results from feeding experiments showed that clearance rates by C. productus during feeding upon non-motile ova were 60% greater than clearance rates during feeding upon swimming gastrulae and prism larvae. Similarly, non-motile heat-killed plutei were captured at significantly greater rates than swimming plutei with identical body sizes and morphology (Table 3). These observations indicate that the development of swimming cilia in D. excentricus contributes to the decreased susceptibility of motile prey stages in a manner that is independent of their encounter rate with C. productus.

4. Dendraster Swimming Behavior

The low susceptibility of Dendraster excentricus plutei in single and mixed-stage feeding experiments appears to depend upon the ability of the plutei to actively avoid capture after they have entered the low Reynolds number hydrodynamic environment immediately surrounding the Cancer productus zoeae. During the transition from prism to pluteus, echinoid larvae develop the ability to reverse the direction of ciliary beating (Mackie et al., 1969; Strathmann et al., 1972). Episodes of ciliary reversal appear to be mediated by contact with objects such as suspended algal cells (Mackie et al., 1969), other larvae, walls of culture containers, or the layer of seawater surface tension (Rumrill, personal observations). Tracings of encounters between D. excentricus plutei and C. productus zoeae indicate that plutei approach the zoeae while swimming in the forward direction. After making contact with the zoea carapace, the plutei reversed the direction of ciliary beating and swam backwards until they were swept away in currents generated by the zoea maxillipeds. High rates of predation upon $MgCl_2$ anesthetized plutei that were inhibited from swimming backwards (Table 3) are consistent with the observations that reversed swimming behavior functions as a post-contact encounter response that reduces the susceptibility of plutei to capture.

Localized episodes of ciliary reversal are utilized by echinoid plutei to capture algal cells (Strathmann, 1971). These small-scale reversals typically involve groups of 18 to 20 cilia. Presumably, larger-scale ciliary reversals that involve major regions of the ciliated band and the locomotory epaulettes are responsible for changes in swimming direction. A network of nerve cells is located along the inner margin of the ciliated band in Dendraster excentricus plutei (Burke, 1983). In plutei of Strongylocentrotus purpuratus the nerve cells are integrated via non-synaptic connections to a series of axonal tracts located beneath the ciliated band (Burke, 1978). Branched microvilli adjacent to the ciliated band and epaulettes make connections with the subciliary nerve cells. The sensory microvilli may detect changes in fluid pressure or deformation rate and induce ciliary reversals as the pluteus approaches an object such as a predatory microcrustacean. Mechanoreceptor microvilli and subciliary nerve cells are absent in gastrula larvae of D. excentricus (Burke, 1983). In the present study, encounter tracings showed that D. excentricus gastrulae typically made repeated contact with the Cancer productus zoeae as they were swept past the carapace and maxillipeds. Repeated contact with C. productus apparently increases the probability of capture by increasing the liklihood that prey will enter the immediate capture sphere of the zoea.

During the planktonic period, stage-specific differences in predation intensity are influenced by stage-specific encounter frequencies and by the probability of capture and escape at each embryonic and larval stage. Estimates of encounter rates between species pairs such as Dendraster excentricus and Cancer productus substantially underestimate the risk due to predation because D. excentricus embryos and larvae are preyed upon by several different types of zooplankton predators

(Pennington et al., 1986). Since the pattern of differential susceptibility to predation observed between D. excentricus and C. productus is applicable to interactions with other microcrustacean predators, D. excentricus appear to be most vulnerable to predation during the early embryonic period because non-motile zygotes and embryos occur in higher densities than later larvae and do not have the behavioral response and handling difficulties of pluteus larvae. Dendraster excentricus plutei are less vulnerable to predation than zygotes and embryos due to their lower densities and post-contact encounter response. These findings suggest that although the planktonic distribution patterns of D. excentricus larvae in nearshore waters appear to be dictated primarily by passive circulation and advective processes (Cameron and Rumrill, 1982; Emlet, 1986), the success or failure of predation attempts is dependent on active larval processes that occur on a much smaller spatial scale.

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CHAPTER III.

EFFECTS OF OVA SIZE, DEVELOPMENT RATE, AND AMBIENT TEMPERATURE ON THE EARLY MORTALITY OF PLANKTOTROPHIC ECHINODERM LARVAE

A. INTRODUCTION

One of the most striking dichotomies recognized by larval biologists is the distinction between exogenous (= planktotrophic) and endogenous (= lecithotrophic) sources of nutrition for developing larvae of benthic marine invertebrates. These contrasting larval trophic modes are typically associated with differences in ova sizes and with subsequent differences in the shape and form of the larval body. Current theoretical concepts of marine invertebrate life history tactics assume that mortality during the larval period is inversely correlated with egg size (Vance 1973; Chia, 1974; Strathmann, 1977; Palmer and Strathmann, 1981). In general, these heuristic models assert that the rate at which zooplankton predators capture and consume invertebrate larvae is inversely proportional to the energy invested in each offspring. Subsequently, it is generally assumed that the high mortality of planktotrophic larvae is offset by a relatively low parental investment per larva (Ayal and Safriel, 1982). Accordingly, life history models predict that planktotrophic invertebrate larvae will be highly susceptible to predation whereas lecithotrophic larvae will be less susceptible. Although indirect comparisons of larval susceptibility between planktotrophic and lecithotrophic species indicate that the assumption of an inverse relationship between ova size and mortality may be valid, the comparisons are indirect because planktotrophic and lecithotrophic larvae are not preyed upon by the same types of carnivorous zooplanktivores (Rumrill, 1987). Comparisons between planktotrophic and lecithotrophic species are also weak because the selective forces that shape invertebrate life histories operate on subtle intraspecific variation in energetic investment and mortality rather than on interspecific differences in these parameters. More direct comparisons can be made of the relationships between ova size and mortality among groups of species that are entirely planktotrophic or lecithotrophic.

Since the susceptibility of marine invertebrate larvae to predation typically changes during ontogeny (Pennington and Chia, 1984; Pennington _et_ _al_., 1986; Rumrill and Chia, 1985; Rumrill _et_ _al_., 1985), variation in the rate of morphogenesis has important consequences concerning the loss of pelagic larval stages to predatory zooplankton. The application of differences in ova size and development rate as indices of mortality depends strongly upon the magnitude and shape of the stage-specific susceptibility curve obtained by investigating predator-prey interactions for particular groups of species (Rumrill _et_ _al_., 1985;

Pennington _et_ _al_., 1986). A corollary to the development rate-mortality concept is that since ambient sea temperature affects rates of larval development, then variability in temperature should also directly affect the duration of the high and low susceptibility periods. Consequently, losses of invertebrate larvae to predatory zooplankton should vary predictably with changes in temperature, particularly during the critical high susceptibility period. As with differences in ova size and development rate, the application of temperature as an index of mortality is also dependent upon the shape of the stage-specific susceptibility curve (Rumrill and Chia, 1985; Rumrill _et_ _al_., 1985).

In this chapter, I report a series of experiments to test the generalizations that losses of planktotrophic echinoderm larvae to predation are related to ova size, temperature and rate of development. Results from this study directly address the assumption of an inverse relationship between development rate and risk, and they lend empirical support to the prevalent view that rapid morphogenesis through the early pre-feeding stages of development should be favored in invertebrate life histories that include a long-lived planktotrophic larval phase.

B. MATERIALS AND METHODS

This research was carried out at Bamfield Marine

Station, on the west coast of Vancouver Island, British Columbia (48°50'N; 125°08'W). Adult echinoderms were collected from intertidal and subtidal habitats near the vicinity of Bamfield Marine Station.

1. Study Organisms

Three species of echinoids, *Strongylocentrotus franciscanus*, *S. purpuratus*, *Dendraster excentricus*, and four species of asteroids, *Pisaster ochraceus*, *Orthasterias koehleri*, *Patiria miniata*, and *Dermasterias imbricata* were used in this study. The species were selected on the basis of availability and because of their range in ova sizes (Table 4). Gametes were obtained either from natural spawning in the laboratory, or by inducing gravid adults to spawn by intracoelomic injections of 0.52 M KCl (echinoids) or 10^{-5} M 1-methyl adenine (asteroids). Larvae were fed *ad libitum* with a 2:1 mixture of *Dunaliella tertiolecta* (Chlorophyta) and *Pavlova leutheri* (Chrysophyta).

Predatory zooplankton used in feeding experiments were all carnivorous crustaceans and included zoea larvae of the brachyuran crab, *Pugettia producta*, the hyperiid amphipod, *Parathemisto pacifica*, and the mysid, *Neomysis rayii*. These particular species of planktonic crustaceans were selected for several reasons. First, all three species co-occur along with planktotrophic echinoderm larvae in surface waters in Barkley Sound (Littlepage, 1971; S. Rumrill, pers. obs.). Second, the species were readily available during the early spring and summer months; *P. producta* zoeae were reared in the laboratory from egg masses obtained from ovigerous female crabs (see Rumrill 1987; Chapter 4). P. pacifica were captured from surface water in oblique zooplankton tows taken with a 125 µm mesh, 0.5 m diameter standard net. N. rayii were captured from schooling swarms with a slurp gun and plastic bags operated by SCUBA divers. Finally, the species were selected because they were known to exhibit a variety of stage-specific predation responses during feeding experiments upon embryos and larvae of planktotrophic echinoderms (Rumrill, personal observations; Pennington et al., 1986).

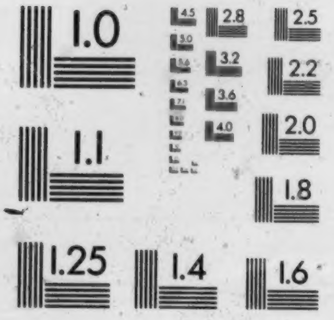
2. Measurements of Ova Size

The diameters of ova were measured to obtain estimates of interspecific and intraspecific variation in ova size. For each species, naturally spawned ova were placed into a Sedgewick-Rafter chamber and the diameters of 100 ova were measured with a calibrated ocular micrometer at a magnification of 40 X. Ova were assumed to be spherical and ova volumes were calculated as Volume = $1/6\,\Pi$ Diameter^3.

3. Effects of Temperature on Development Rates

Ova of each echinoderm species were fertilized with a dilute sperm suspension, and the zygotes were raised in 1000 ml glass beakers. Cultures of embryos and larvae were maintained at 3 temperatures in laboratory incubators under a 16L:8D photoperiod regime. A maximum-minimum thermometer indicated that temperatures in the incubators fluctuated by about ± 3°C, so the cultures experienced thermal regimes

2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2.0
1.1
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1.25
1.4
1.6

of 8 ± 2, 12 ± 2, and 15 ± 2°C. Embryo and larval cultures were agitated with a slow stream of small air bubbles supplied through intramedic surgical tubing. Cultures were examined every 2 hrs during the first 20 hrs following fertilization and every 8 hrs after hatching.

4. Predation by Zooplanktonic Crustaceans

Susceptibility of echinoderm embryos and larvae to predation was examined in the laboratory in a series of microcosm feeding experiments. The methods used in the feeding experiments were similar to those reported by Rumrill *et al*. (1985; Chapter 3), although a mixing apparatus was used that could simultaneously process up to 36 replicate predator-prey microcosms.

Functional response feeding experiments were carried out to determine the effects of changes in prey density on rates of predation. Feeding experiments were conducted at 6 different prey concentrations (10, 25, 50, 100, 150, and 250 prey $liter^{-1}$). Ova were obtained from each species of echinoderm, inseminated with a dilute sperm suspension, and washed several times to remove excess sperm. The zygotes were placed into 1 liter glass jars filled with 1 µm filtered seawater, a single predatory crustacean was added, and the jars were sealed and attached to the mixing apparatus. All functional response experiments were conducted at 12 ± 2°C in an incubator with 16L:8D photoperiod. Each feeding experiment consisted of 8 replicate predator treatments and 4 controls without predators. The duration of each experiment was 12 hours, so the echinoderm zygotes developed through the early cleavage stages to late un-hatched morulae during the course of each experiment. The entire series of functional response experiments required over 9 weeks to complete, although predation experiments at increasing prey densities were always conducted on successive days for any particular species of prey. All functional response experiments with *Neomysis rayii* were conducted over a period of 19 days.

Stage-specific differences in larval susceptibility were examined for each species of echinoderm in microcosm feeding experiments conducted at an initial prey density of 50 prey liter^{-1}. The 6 categories of prey used in the majority of experiments of feeding upon echinoids were: 1) unfertilized ova~~, 2) non-motile~~ embryos, 3) motile blastulae and gastrulae, 4) prism larvae, 5) 4-armed plutei, and 6) 6-armed plutei. Trials with eight armed plutei were also conducted in feeding experiments with *Pugettia producta*. In the asteroids, feeding experiments were carried out with 6 categories of prey: 1) unfertilized ova, 2) non-motile embryos, 3) motile blastulae and early gastrulae, 4) late gastrulae, 5) early bipinnaria larvae, and 6) brachiolaria larvae. Feeding experiments were conducted with a homogeneous group of single prey stages for all 7 species of echinoderms. Feeding experiments were also carried out with heterogeneous mixtures of *Strongylocentrotus franciscanus* developmental stages. All stage-specific susceptibility experiments were were carried out in an incubator at 12 ± 2°C. Each series of experiments was terminated after a period of 12 hrs.

Because the development rates of all 7 species of echinoderms were responsive to differences in ambient temperature, a series of feeding experiments were conducted under different thermal conditions to determine how variation in development rates affects the susceptibility of embryos and larvae to predation during the planktonic period. A series of long-term feeding experiments were conducted to analyse the effects of predation by *Pugettia producta* at different temperatures. One hundred and fifty zygotes from each of the seven species of echinoderms were placed into 1 liter glass jars filled with 1 µm filtered seawater. At the beginning of each experiment a single stage I zoea larva of *P. producta* was placed into the jar. The jars were sealed and attached to the rotating mixing device. Each set of trials consisted of 5 replicate predator treatments and 3 controls without predators. The experiments were terminated after a period of 120 hrs. Separate sets of feeding experiments were conducted at 8 ± 2, 12 ± 2 and 15 ± 2°C. Although seawater in the jars was not replenished during the course of the experiments, the zoeae and remaining echinoderm larvae appeared in good health when they were examined at the end of the experiments.

Additional feeding experiments were conducted at 5 temperatures (8, 10, 12, 14, 16°C) to assess the effects of temperature on rates of Pugettia producta predation upon embryos of Strongylocentrotus franciscanus and Pisaster ochraceus. These experiments were composed of between 6 and 10 replicate predator treatments and 3 to 5 controls without predators. The initial density of prey items was 100 embryos liter^{-1}, and each feeding trial lasted 12 hrs.

C. RESULTS

1. Variation in Ova Size

Interspecific and intraspecific variation in the sizes of echinoderm ova are summarized in Table 4. Ova sizes among the 7 planktotrophic echinoderm species ranged from 85 µm to 172 µm in diameter and from 0.32 X 10^6 to 2.7 X 10^6 µm^3 in volume. Thus, ova diameters varied by a factor of 2 between Strongylocentrotus purpuratus and Dermasterias imbricata, and the volume of individual ova varied by a factor of 8 between these two species (Table 4). Size-frequency analysis of ova diameters indicated that all populations of ova were unimodal. However, coefficients of variation were generally greatest for species with small ova (S. purpuratus, Dendraster excentricus) and suggest that greater variability in ova sizes occurred among samples of ova collected from species with small eggs.

Table 4

Comparison of the diameters and volumes of naturally spawned ova from seven species of echinoderms. Sample size is 100 ova for each species. Table entries show means; standard deviations are indicated in parentheses. CV columns indicate coefficients of variation. Scaling column shows scale relationships for diameter and volume in comparisons with ova from *Strongylocentrotus purpuratus*.

SPECIES	DIAMETER (µm)	C.V. (%)	VOLUME ($10^6 \mu m^3$)	C.V. (%)	SCALING dia / vol
Strongylocentrotus purpuratus	84.6 (4.7)	5.6	0.32 (0.06)	17.4	1 / 1
Strongylocentrotus franciscanus	152.1 (4.3)	2.8	1.84 (0.15)	8.1	1.8 / 5.7
Dendraster excentricus	120.1 (6.4)	5.3	0.91 (0.14)	15.9	1.4 / 2.8
Pisaster ochraceus	160.1 (5.5)	3.4	2.16 (0.22)	10.4	1.9 / 6.7
Orthasterias koehleri	139.1 (5.2)	3.7	1.40 (0.21)	14.8	1.6 / 4.4
Patiria miniata	136.7 (5.6)	4.1	1.34 (0.17)	12.46	1.6 / 4.2
Dermasterias imbricata	171.6 (6.5)	3.8	2.66 (0.29)	11.05	2.0 / 8.3

2. Effects of Temperature on Development Rates

Measurements of embryo and larval development rates in laboratory cultures showed that there was substantial interspecific and intraspecific variability in the time needed for planktotrophic echinoderm larvae to reach particular stages of development. The majority of embryos and larvae developed at nearly identical rates, but a portion of the population exhibited retarded rates of morphogenesis compared with others in the same culture vessel.

The development rates of all 7 species of echinoderms were dependent upon temperature. Figures 5 and 6 show the time in hours needed to reach various larval stages in laboratory cultures. The time necessary to develop into the first feeding (4-armed pluteus or bipinnaria) larval stages was greatest at 8°C, intermediate at 12°C and shortest at 15°C. Thermal-induced acceleration and retardation of development rates gave Q_{10} values between 1.7 (Patiria miniata) and 2.5 (Pisaster ochraceus). These results indicate that rates of morphogenesis differ among planktotrophic species, and that further intraspecific variation in development rates can be induced by differences in culture temperature that approximate the range of temperatures found in the field.

One of the consequences of variation in ova sizes is a partial correlation with the rate of development to a feeding larval stage. Two comparisons are valid at the

Figure 5. Development rates of echinoid embryos and larvae. Points show the number of hours necessary for zygotes to develop to a particular developmental stage at temperatures of 8 ± 2, 12 ± 2 and 15 ± 2°C. B = unhatched blastula; H = hatching; G = gastrula; Pr = prism larva; P4 = 4-arm pluteus. Dashed lines and numbers on the right side of the figure provide an example of the increased time needed to reach the 4-arm pluteus stage by zygotes of *Strongylocentrotus purpuratus* at 8°C compared to 15°C.

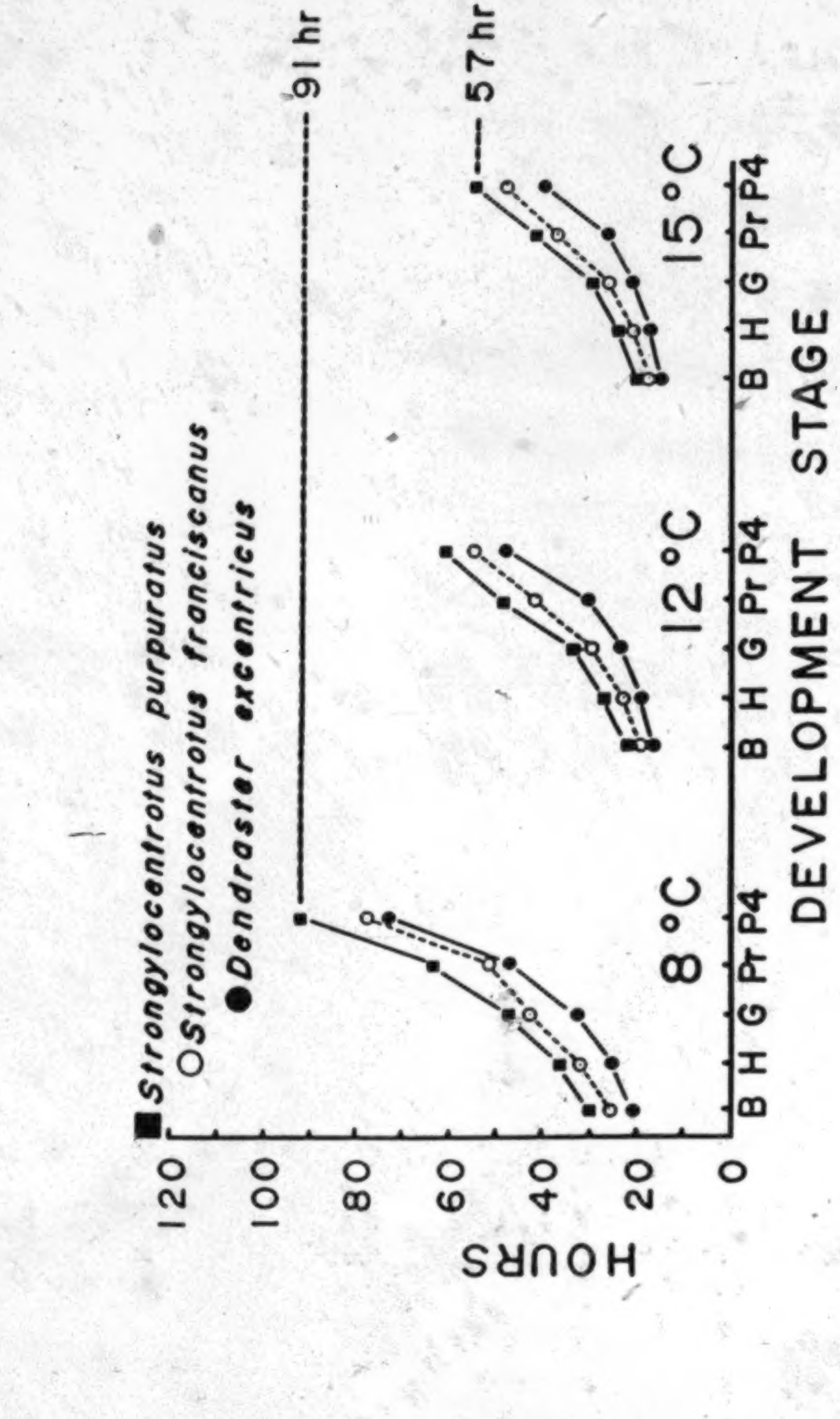
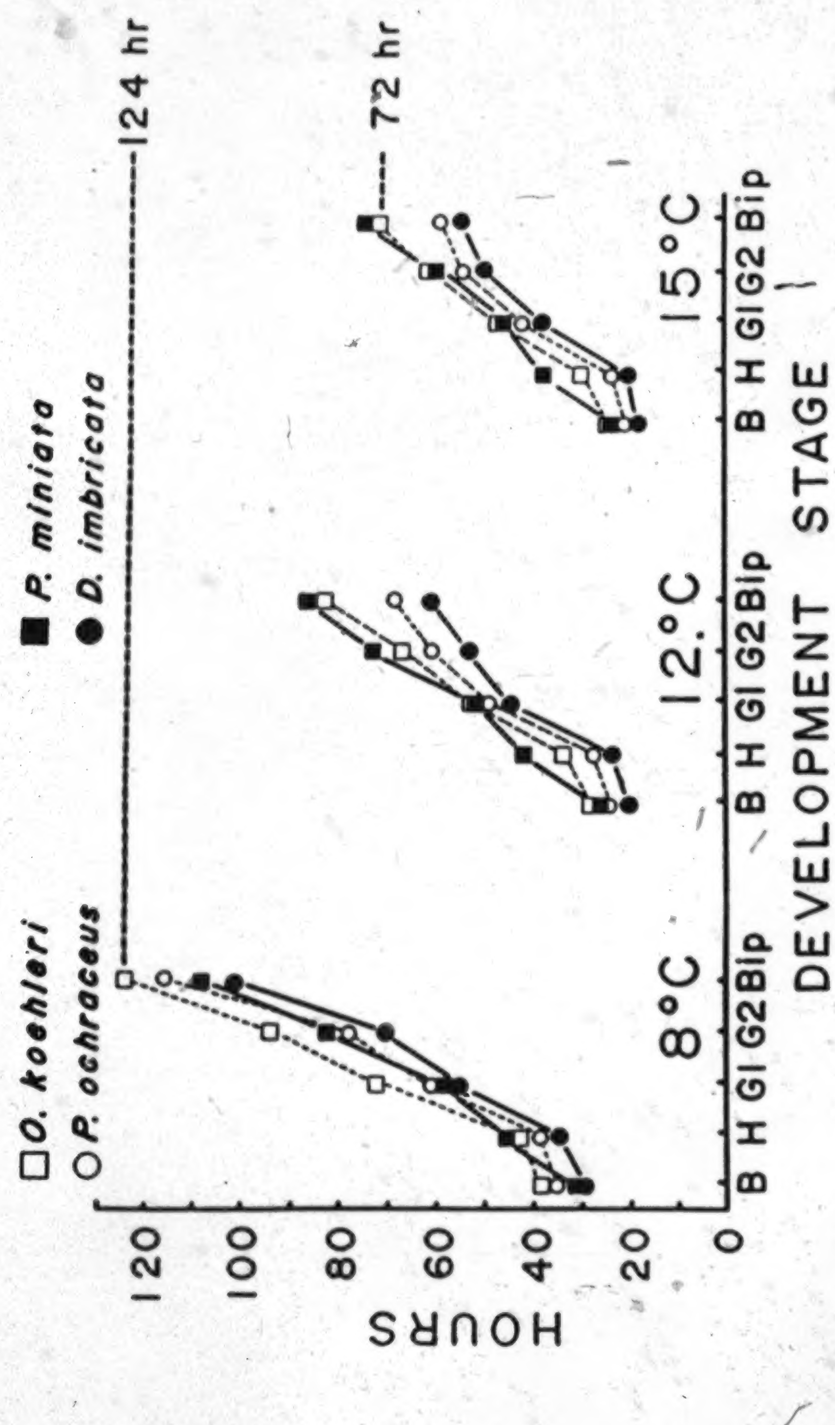

■ Strongylocentrotus purpuratus
○ Strongylocentrotus franciscanus
● Dendraster excentricus
HOURS
120
100
80
60
40
20
0
91 hr
57 hr
B H G Pr P4
8 °C
B H G Pr P4
12 °C
B H G Pr P4
15 °C
DEVELOPMENT STAGE

Figure 6. Development rates of asteroid embryos and larvae. Points show the number of hours necessary for zygotes to develop to a particular developmental stage at temperatures of 8 ± 2, 12 ± 2 and 15 ± 2°C. B = unhatched blastula; H = hatching; G1 = early gastrula; G2 = late gastrula; Bip = bipinnaria larva. Dashed lines and numbers on the right side of the figure provide an example of the increased time needed to reach the bipinnaria stage by zygotes of _Orthasterias_ _koehleri_ at 8°C compared to 15°C.


□ O. koehleri
○ P. ochraceus
■ P. miniata
● D. imbricata
124 hr
72 hr
HOURS
0
20
40
60
80
100
120
B H G1 G2 Bip
8°C
B H G1 G2 Bip
12°C
B H G1 G2 Bip
15°C
DEVELOPMENT STAGE

familial level, and three are warranted at the ordinal level. First, within the strongylocentrotid urchins (order echinoida) development rate to a feeding 2-armed pluteus increased with increasing ova diameter (Table 4, Figure 5). The development of *Strongylocentrotus purpuratus* (ova diam = 84.6 µm) was consistently slower than that of *S. franciscanus* (ova diam = 152.1 µm) at all three temperatures. Second, the rate of development to a feeding bipinnaria larval stage also increased with ova diameter in the two asterid sea stars, *Pisaster ochraceus* and *Orthasterias koehleri* (order forcipulatida). Similarly, the time needed to reach the bipinnaria stage also increased with decreasing ova size in the remaining sea stars (order spinulosida). The rapid development of *Dendraster excentricus* (ova diam = 120.1 µm, order clypeasteroida) is inconsistent with the prediction from ova diameter, and is comparable to the rapid morphogenesis reported for other clypeasteroids (Kume and Dan, 1968). These comparisons indicate: 1) the echinoids develop to a feeding larval stage at a relatively rapid rate compared with the asteroids, and 2) consideration must be given to the taxonomic position of species in evaluating correlations between ova size and development rate.

3. Predation by Zooplanktonic Crustaceans

Predator-prey interactions between planktotrophic echinoderm larvae and zooplanktonic crustaceans have several components. These include: a) the functional response of predators to increasing prey density, b) differences in the susceptibility of various developmental stages to capture and ingestion, and c) the effects of differences in development rates on the total number of embryos and larvae captured.

a. Functional Response of Predation

The functional responses of crustacean predators to increases in embryo density are shown in Figures 7-9. Predation rates by *Pugettia producta*, *Parathemisto pacifica* and *Neomysis rayii* all increased with increasing embryo density. Although predation rates increased consistently over the range of prey densities offered (ANOVA, $p < 0.001$), the relatively slower rate of increase at high embryo densities suggests that *P. producta*, *P. pacifica* and *N. rayii* all exhibit Holling (1966) Type II functional response curves during feeding upon planktotrophic echinoderm embryos. Most of the plots showed evidence that feeding approached saturation rates at prey densities greater than 150 embryos liter^{-1}. Rates of predation were inversely correlated with ova volume when the results of feeding experiments conducted at initial prey densities of 150 embryos liter^{-1} were compared among all 7 species of echinoderms (*P. producta*: Kendall's tau = -0.4106, n = 56, $p < 0.001$; *P. pacifica*: tau = -0.2628, n = 56, p = 0.0034; *N. rayii*: tau = -0.3991, n = 56, $p < 0.001$).

b. Stage-Specific Susceptibility

Stage-specific differences in the susceptibility of

Figure 7. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon echinoid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Strongylocentrotus franciscanus* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.06X^{0.68}$, $r^2 = 0.83$ (ANOVA, F-ratio = 43.11, $p<0.001$). *Pugettia*: $Y = 0.09X^{0.66}$, $r^2 = 0.91$ ($F = 46.01$, $p<0.001$). *Neomysis*: $Y = 0.08X^{0.81}$, $r^2 = 0.96$ ($F = 73.34$, $p<0.001$). B. Predation upon *Strongylocentrotus purpuratus* embryos. *Parathemisto*: $Y = 0.07X^{0.74}$, $r^2 = 0.88$ ($F = 58.07$, $p<0.001$). *Pugettia*: $Y = 0.07X^{0.83}$, $r^2 = 0.95$ ($F = 109.08$, $p<0.001$). *Neomysis*: $Y = 1.40X^{0.84}$, $r^2 = 0.97$ ($F = 144.08$, $p<0.001$). C. Predation upon *Dendraster excentricus* embryos. *Parathemisto*: $Y = 0.09X^{0.66}$, $r^2 = 0.89$ ($F = 61.36$, $p<0.001$). *Pugettia*: $Y = 0.07X^{0.78}$, $r^2 = 0.93$ ($F = 60.34$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.90}$, $r^2 = 0.94$ ($F = 176.19$, $p<0.001$).

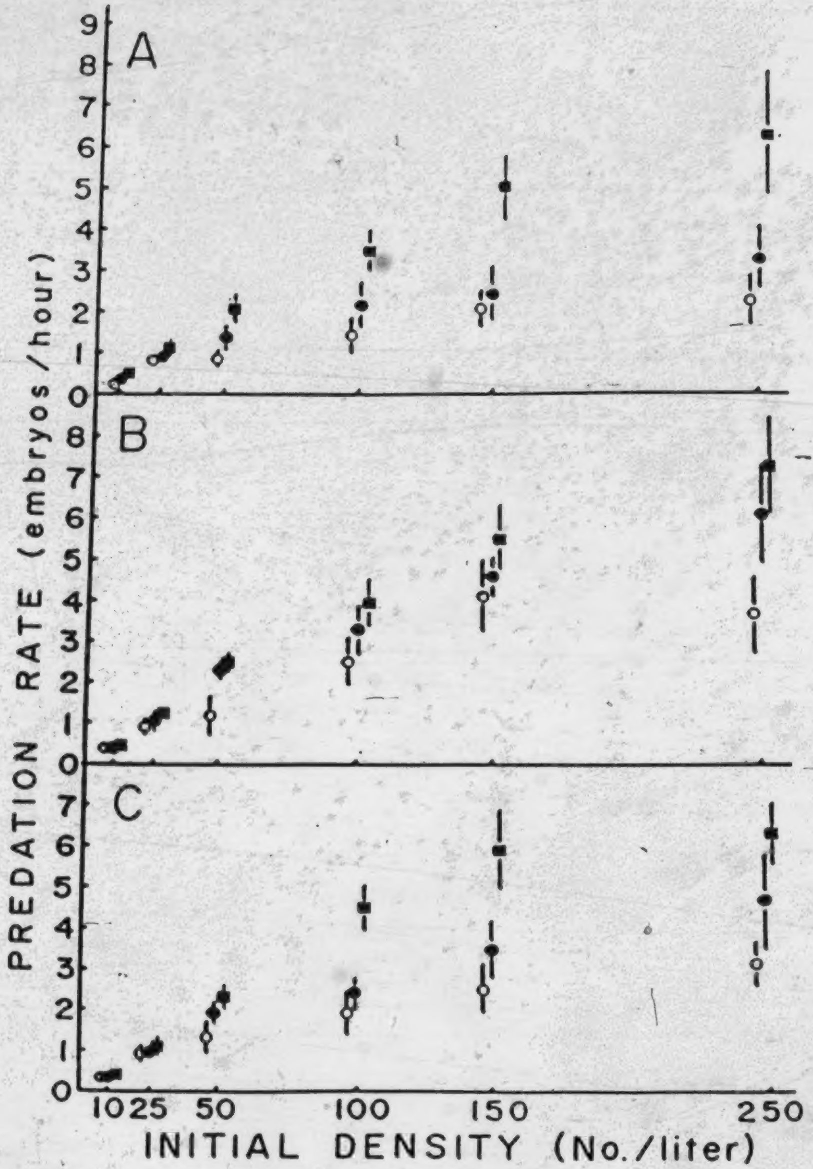

A
B
C
PREDATION RATE (embryos/hour)
0
1
2
3
4
5
6
7
8
9
10
25
50
100
150
250
INITIAL DENSITY (No./liter)

Figure 8. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon asteroid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Pisaster ochraceus* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.08X^{0.72}$, $r^2 = 0.92$ (ANOVA, F-ratio = 96.51 $p<0.001$). *Pugettia*: $Y = 0.08X^{0.73}$, $r^2 = 0.95$ ($F = 101.81$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.86}$, $r^2 = 0.95$ ($F = 107.97$, $p<0.001$). B. Predation upon *Orthasterias koehleri* embryos. *Parathemisto*: $Y = 0.06X^{0.82}$, $r^2 = 0.94$ ($F = 152.53$, $p<0.001$). *Pugettia*: $Y = 0.06X^{0.86}$, $r^2 = 0.97$ ($F = 148.61$, $p<0.001$). *Neomysis*: $Y = 0.06X^{0.90}$, $r^2 = 0.97$ ($F = 200.34$, $p<0.001$).

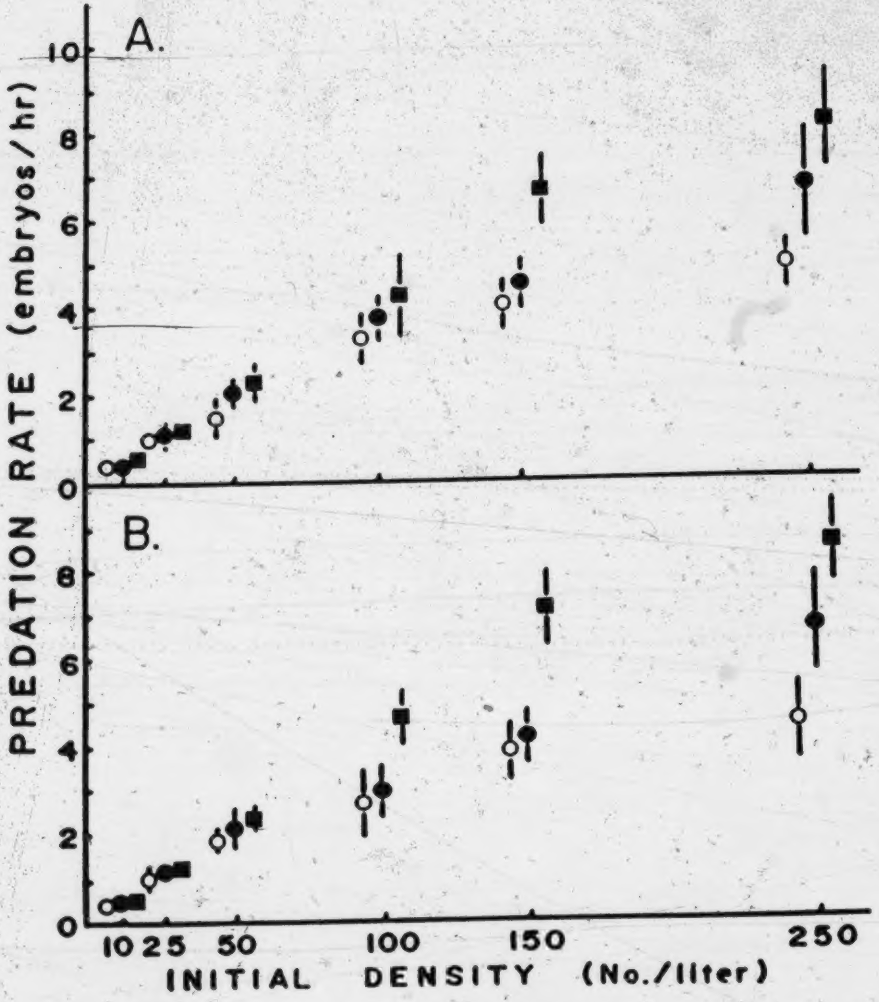
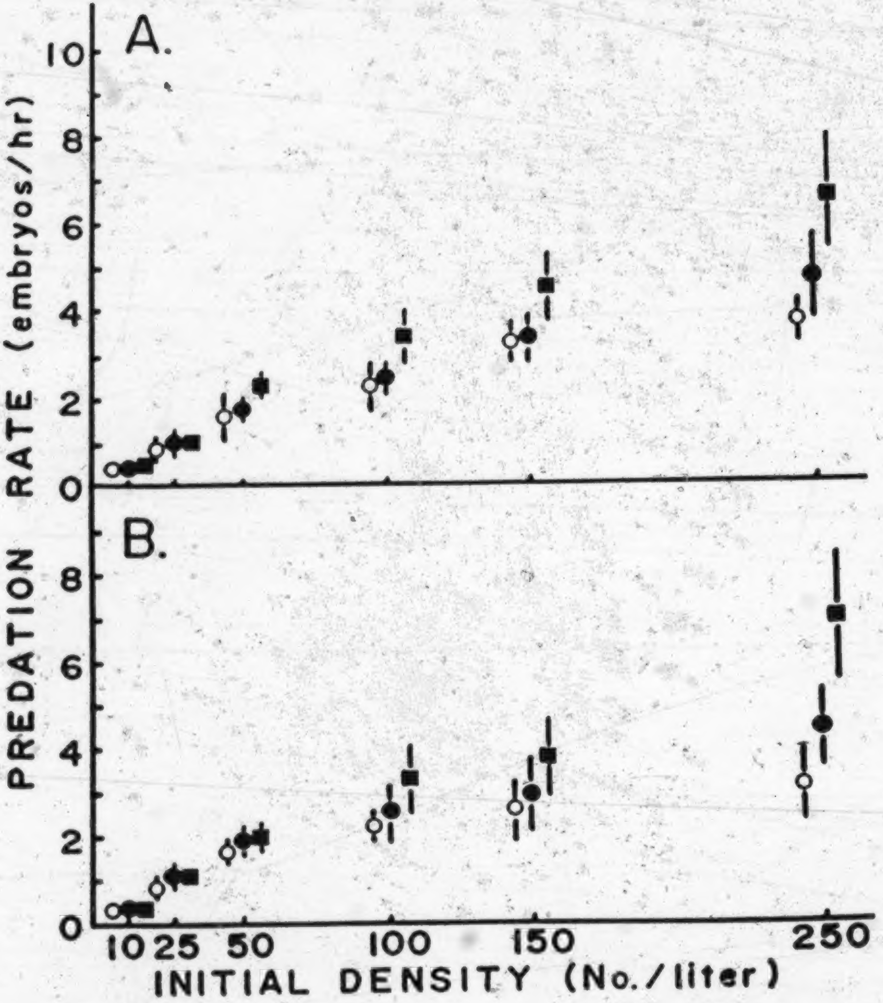

A.
B.
PREDATION RATE (embryos/hr)
0
2
4
6
8
10
10
25
50
100
150
250
INITIAL DENSITY (No./liter)

Figure 9. Functional response of predation by *Parathemisto pacifica* (○), *Pugettia producta* (●), and *Neomysis rayii* (■) upon asteroid embryos. Values show means, error bars indicate ± 1 s.d. A. Predation upon *Patiria miniata* embryos. *Parathemisto* functional response is best fit by the least squares regression equation $Y = 0.09X^{0.73}$, $r^2 = 0.94$ (ANOVA, F-ratio = 84.29 $p<0.001$). *Pugettia*: $Y = 0.07X^{0.81}$, $r^2 = 0.97$ ($F = 133.39$, $p<0.001$). *Neomysis*: $Y = 0.05X^{0.97}$, $r^2 = 0.98$ ($F = 358.68$, $p<0.001$). B. Predation upon *Dermasterias imbricata* embryos. *Parathemisto*: $Y = 0.09X^{0.67}$, $r^2 = 0.91$ ($F = 57.42$, $p<0.001$). *Pugettia*: $Y = 0.09X^{0.72}$, $r^2 = 0.90$ ($F = 61.85$, $p<0.001$). *Neomysis*: $Y = 0.07X^{0.81}$, $r^2 = 0.95$ ($F = 89.30$, $p<0.001$).


A.
B.
PREDATION RATE (embryos/hr)
0
2
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6
8
10
INITIAL DENSITY (No./liter)
10
25
50
100
150
250

echinoderm embryos and larvae were evident during the predation experiments. The most complete sets of data were gathered for *Strongylocentrotus franciscanus* and *Pugettia producta*. In the feeding experiments with *P. producta*, rates of predation upon ova, embryos and early larval stages were greater than rates of predation upon later 4, 6, and 8 armed pluteus stages (Figure 10). These stage-specific differences in the susceptibility of *S. franciscanus* developmental stages to predation were consistent between single-stage and mixed-stage feeding experiments (Figure 10). Stage-specific differences in susceptibility were also observed during the ontogeny of *S. franciscanus* during predation experiments conducted with *Parathemisto pacifica* (Figure 11). However, motile blastulae and prism stage larvae were captured at a greater rate than earlier ova and embryos and later pluteus larval stages (Figure 11). As in *P. producta*, there was no difference in the shape of the stage-specific susceptibility curve during experiments conducted with single and mixed prey stages. Finally, stage-specific differences in the susceptibility of *S. franciscanus* during single-stage feeding experiments conducted with *Neomysis rayii* (Figure 12a) were similar to the pattern observed earlier during single and mixed prey experiments with *P. producta* (Figure 10). However, predation rates upon 4 and 6-armed pluteus larval stages were greater than predation rates upon ova, embryos and early larval stages

Figure 10. Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus* by *Pugettia producta*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls.
OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae,
PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus, PL8 = 8-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.

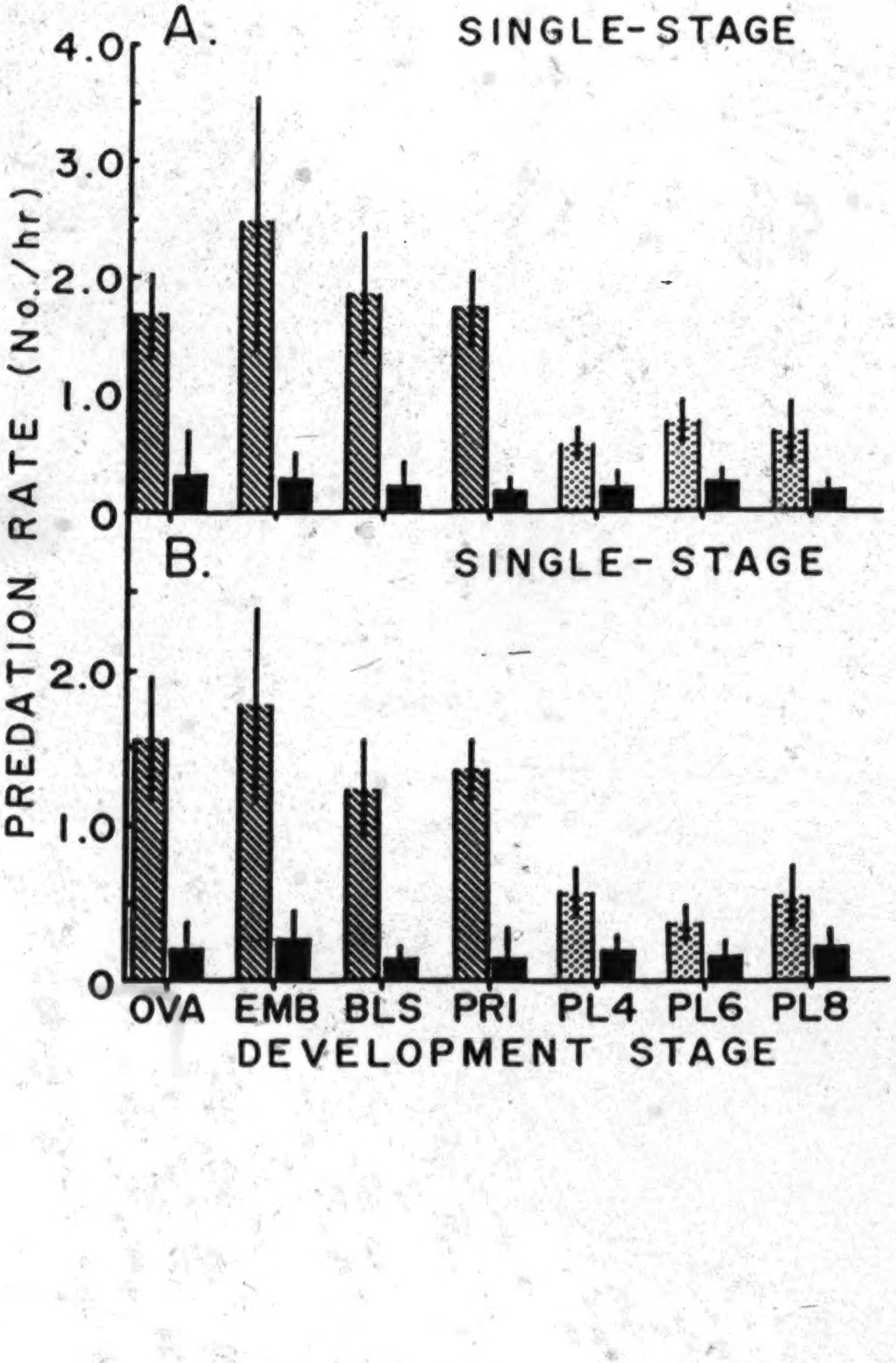

A.
SINGLE-STAGE
B.
SINGLE- STAGE
PREDATION RATE (No./hr)
4.0
3.0
2.0
1.0
0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
PL8
DEVELOPMENT STAGE

Figure 11. Differential rates of predation upon developmental stages of *Strongylocentrotus franciscanus* by *Parathemisto pacifica*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls.
OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae,
PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.

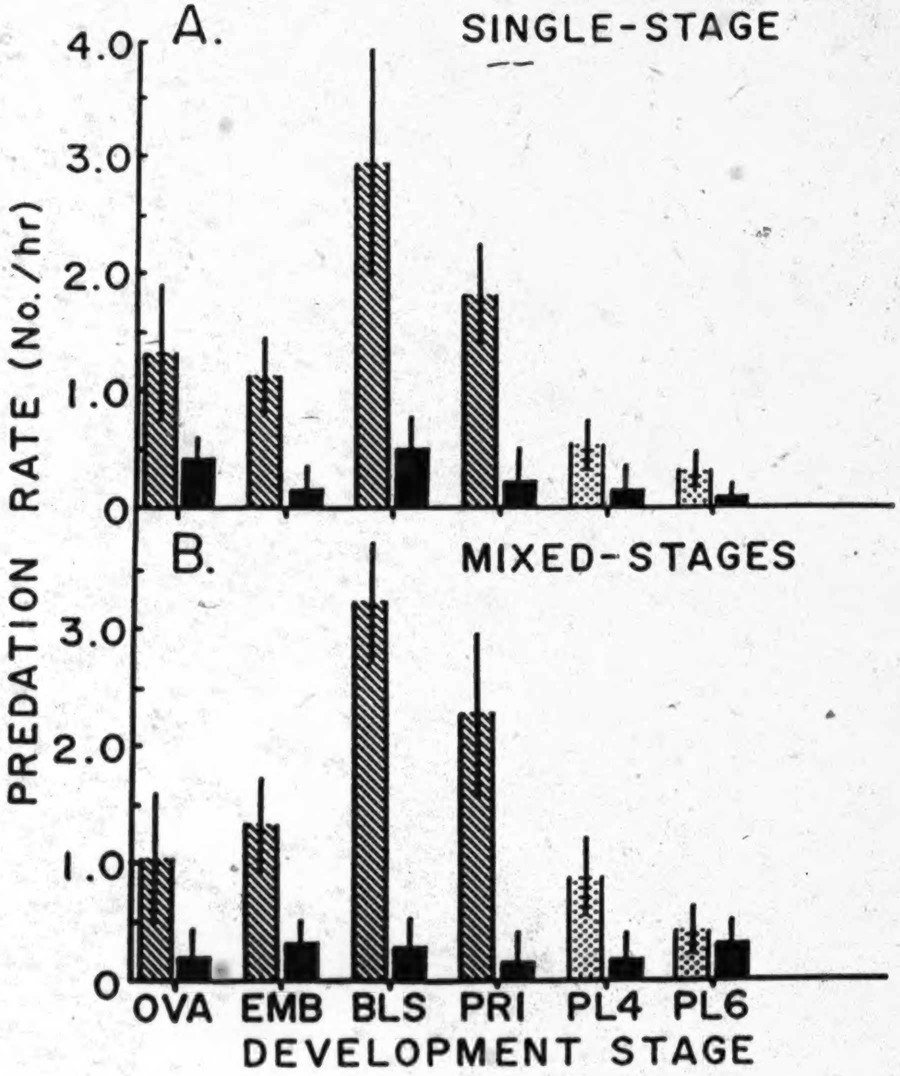
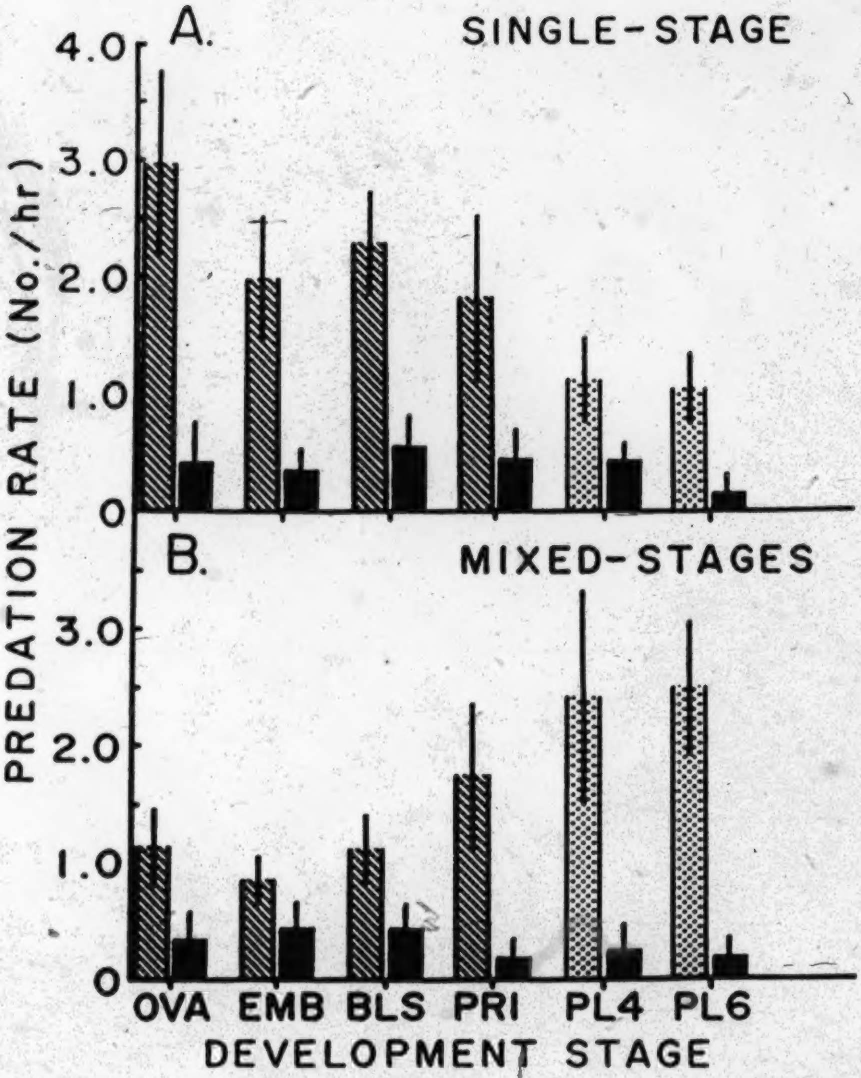

A.
SINGLE-STAGE
B.
MIXED-STAGES
PREDATION RATE (No./hr)
4.0
3.0
2.0
1.0
0
3.0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
DEVELOPMENT STAGE

Figure 12. Differential rates of predation upon developmental stages of Strongylocentrotus franciscanus by Neomysis rayii. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae, PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates during single prey stage feeding experiments. B. Predation rates during mixed prey stage feeding experiments.

1


A.
SINGLE-STAGE
4.0
3.0
2.0
1.0
0
B.
MIXED-STAGES
3.0
2.0
1.0
0
PREDATION RATE (No./hr)
OVA
EMB
BLS
PRI
PL4
PL6
DEVELOPMENT STAGE

when N. rayii were offered a heterogeneous assemblage of mixed S. franciscanus developmental stages (Figure 12b). In this case the proportion of particular S. franciscanus developmental stages offered to N. rayii was experimentally decreased from 100% in the single-stage trials to 33% in the mixed-stage trials. Further experiments with intermediate prey proportions are neccessary to determine the extent of prey switching by N. rayii.

Stage-specific differences in the susceptibility of embryos and larvae were also observed during predation by Pugettia producta upon developmental stages of 4 other species of echinoderms. Ova, embryos and early larval stages of Strongylocentrotus franciscanus and Dendraster excentricus were preyed upon at a greater rate than later pluteus larvae (Figure 13). Similarly, ova, embryos and early gastrula I and gastrula II larval stages of Pisaster ochraceus and Orthasterias koehleri were also more susceptible to predation by P. producta than the later bipinnaria and brachiolaria stages (Figure 14).

c. Long-Term Predation Experiments

The results of the long-term predation experiments with Pugettia producta are shown in Table 5. Predation rates upon echinoderm developmental stages were consistently greatest for all species of echinoderms at 8°C. In the majority of cases predation rates were intermediate at 12°C and lowest at 15°C. Although the relationship between predation rate and temperature may be due in part

Figure 13. Differential rates of predation upon developmental stages of _Strongylocentrotus_ _purpuratus_ and _Dendraster_ _excentricus_ by _Pugettia_ _producta_. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding pluteus larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, BLS = hatched motile blastulae, PRI = prism larvae, PL4 = 4-armed pluteus, PL6 = 6-armed pluteus. A. Predation rates upon _Strongylocentrotus_ _purpuratus_ during single prey stage feeding experiments. B. Predation rates upon _Dendraster_ _excentricus_ during single prey stage feeding experiments.

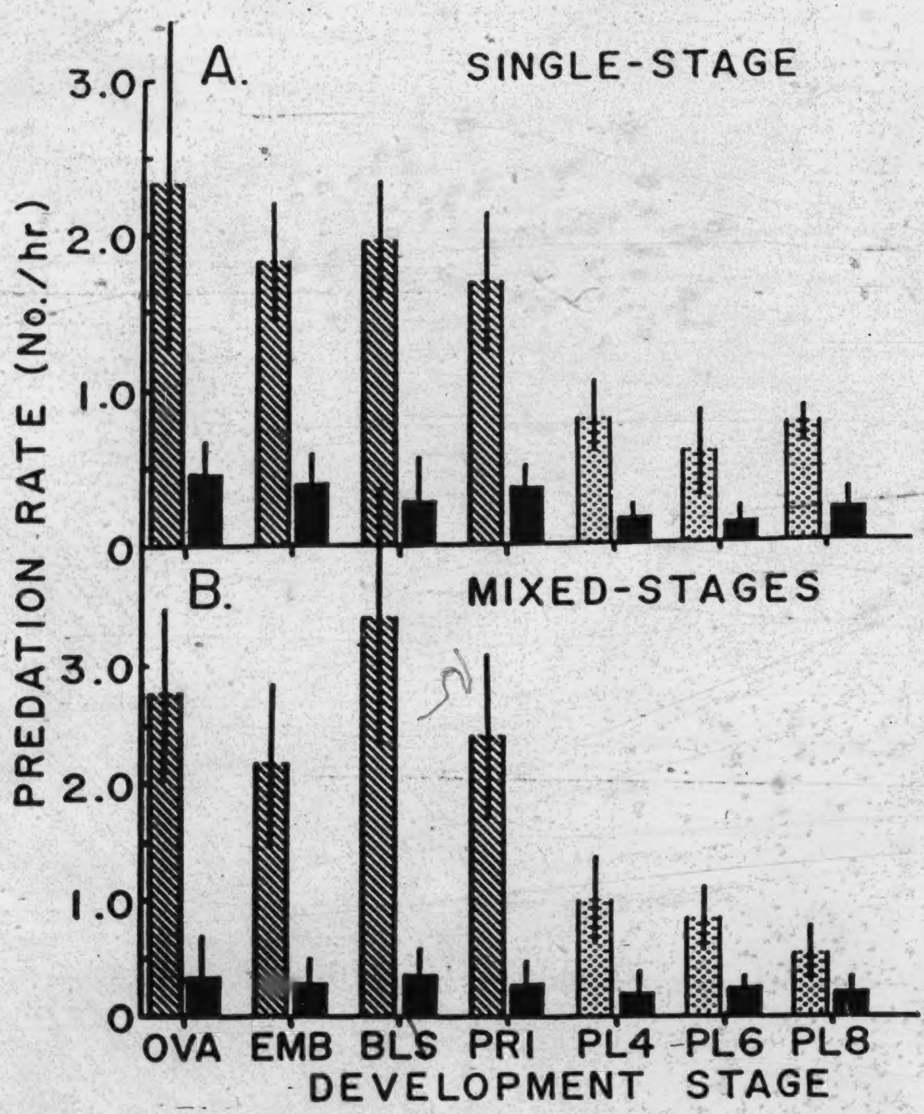

A.
SINGLE-STAGE
B.
MIXED-STAGES
PREDATION RATE (No./hr.)
3.0
2.0
1.0
0
OVA
EMB
BLS
PRI
PL4
PL6
PL8
DEVELOPMENT STAGE

Figure 14. Differential rates of predation upon developmental stages of *Pisaster ochraceus* and *Orthasterias koehleri* by *Pugettia producta*. Values indicate means, error bars indicate ± 1 s.d. Slashed bars show predation rates upon pre-feeding ova, embryos and early larval stages. Stippled bars show predation rates upon feeding bipinnaria and brachiolaria larvae. Solid bars indicate losses of prey in controls. OVA = unfertilized ova, EMB = zygotes through unhatched embryonic stages, GS1 = early gastrula, GS2 = late gastrula larvae, BIP = bipinnaria, BCH = brachiolaria. A. Predation rates upon *Pisaster ochraceus* during single prey stage feeding experiments. B. Predation rates upon *Orthasterias koehleri* during single prey stage feeding experiments.

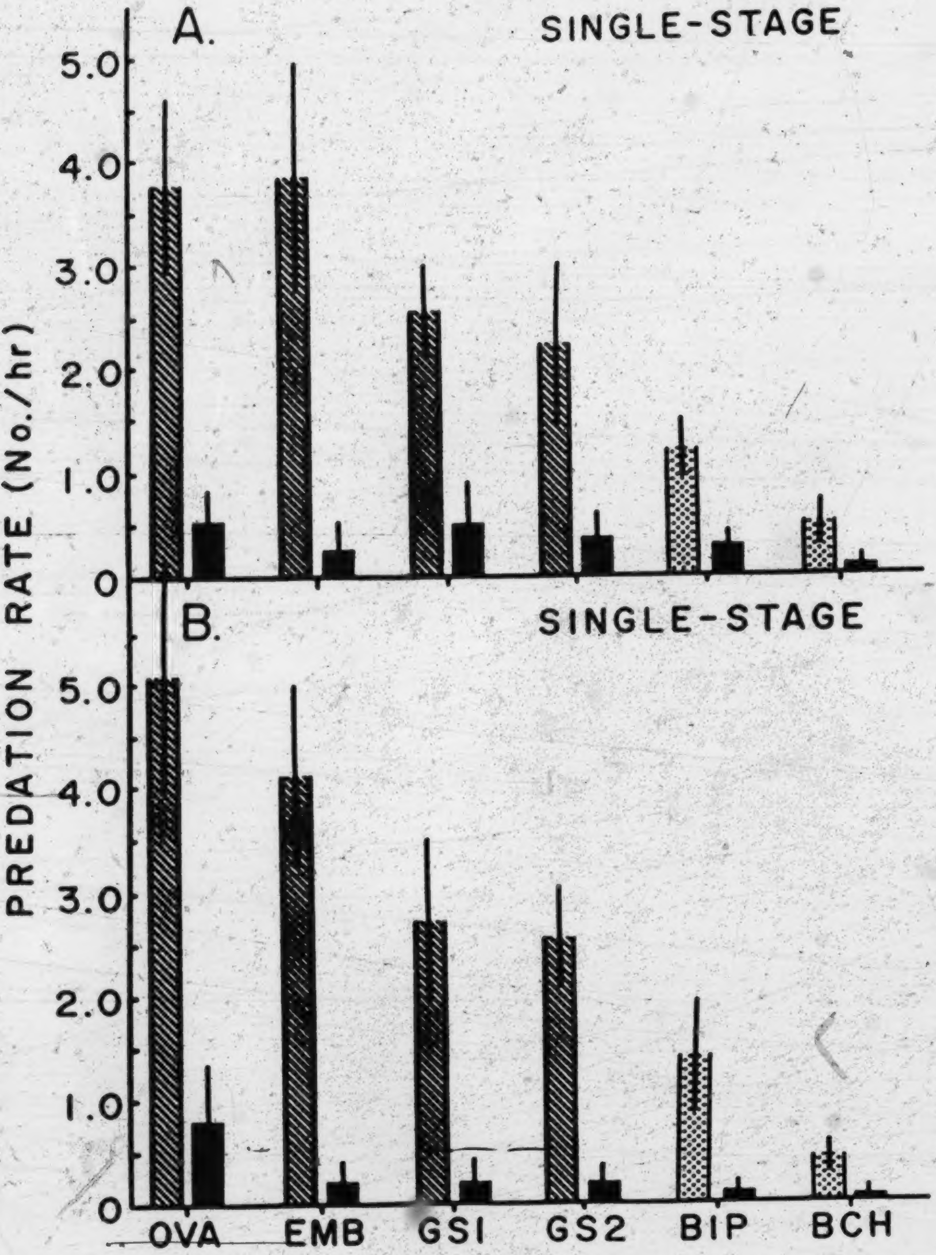

A.
SINGLE-STAGE
B.
SINGLE-STAGE
PREDATION RATE (No./hr)
5.0
4.0
3.0
2.0
1.0
0
OVA
EMB
GS1
GS2
BIP
BCH

Table 5

Predation rates by Pugettia producta zoeae upon embryos and larvae of seven planktotrophic echinoderms during long-term feeding experiments. Table entries show mean (± s.d.) from 5 replicate predator treatments in experiments carried out at 8, 12 and 15°C. The initial density of prey was 150 embryos liter^{-1}.

Genus species	TEMPERATURE °C	# HOURS TO FEEDING STAGE	# PREY STAGES CONSUMED / 24 HRS
Strongylocentrotus franciscanus	8	77	16 ± 3
	12	55	11 ± 1
	15	49	10 ± 1
Strongylocentrotus purpuratus	8	91	19 ± 2
	12	60	17 ± 2
	15	54	13 ± 1
Dendraster excentricus	8	74	14 ± 2
	12	49	12 ± 2
	15	41	9 ± 1
Pisaster ochraceus	8	116	23 ± 2
	12	69	16 ± 3
	15	60	14 ± 3
Orthasterias koehleri	8	124	23 ± 3
	12	84	15 ± 2
	15	74	17 ± 2
Patiria miniata	8	109	21 ± 3
	12	88	16 ± 3
	15	76	16 ± 3
Dermasterias imbricata	8	103	19 ± 3
	12	63	15 ± 3
	15	57	12 ± 2

to differences in the metabolic demands upon P. producta zoeae, the clearance rate of zoeae did not change over a range of temperatures from 8 to 16°C (Figure 15). In contrast to the relationship observed previously during functional response experiments (Figures 7-9), predation rates by P. producta were not correlated with the initial size of their prey items during the long-term experiments (Table 6). The difference between these results is not due to differences in initial prey density since both sets of data are drawn from experiments conducted at densities of 150 embryos liter^{-1}. It is likely that the correlation between ova volume and predation rate is significantly negative during the functional response experiments because the zoeae fed rapidly upon abundant prey for a relatively short period of time (12 hrs). In contrast, zoeae may have fed rapidly during the initial hours of the long-term experiment, but in this case the predation rates reflect feeding averaged over a period of 120 hrs. Presumably zoeae were well below saturation feeding rates during the latter part of the long-term feeding experiments.

Predation rates were strongly correlated with the development rates of their respective prey species (Table 6, Figure 16). The correlation between embryo-larval mortality and development rate was highly significant when data from all three temperatures were considered ($p < 0.001$). Furthermore, the relationship was also significant when predation rates from experiments conducted at a single

Figure 15. Clearance rates of *Pugettia producta* zoeae during predation upon *Strongylocentrotus franciscanus* (●) and *Pisaster ochraceus* (○) embryos. Values show means, error bars indicate ± 1 s.d. The numbers above each temperature indicate sample sizes (echinoids / asteroids).

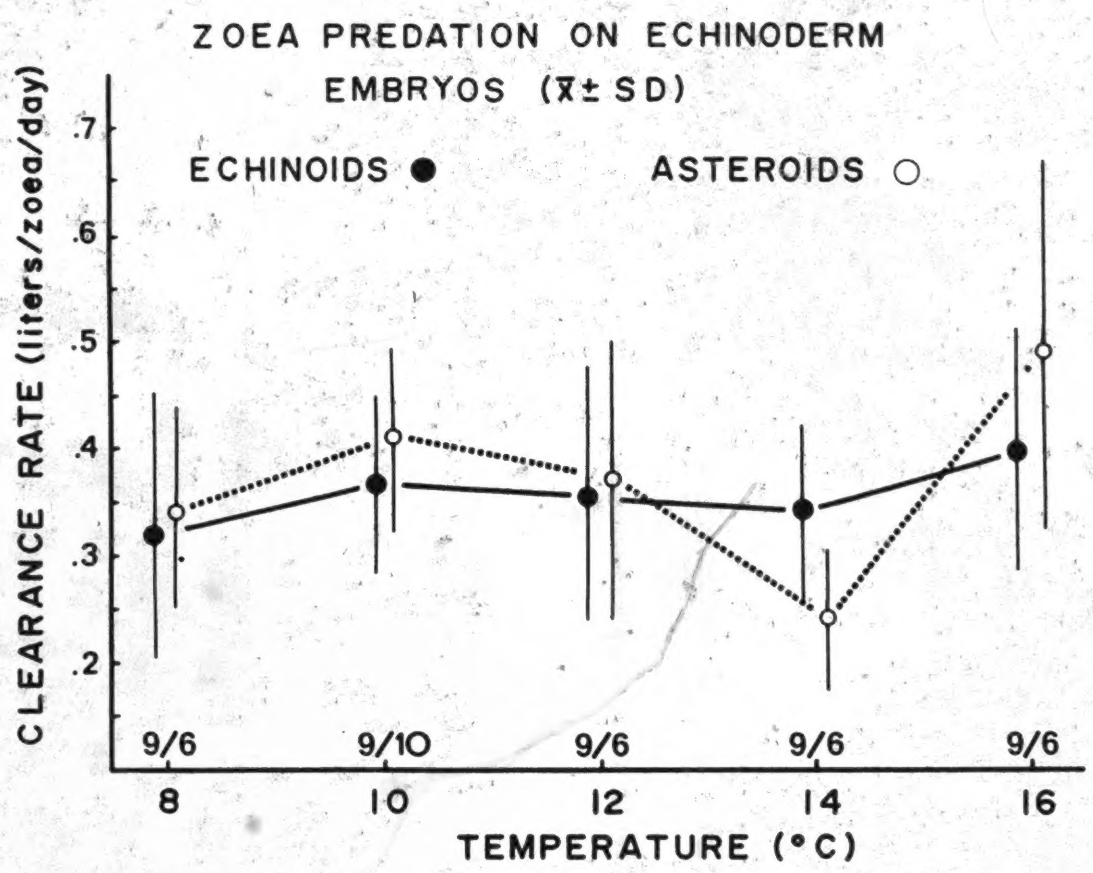
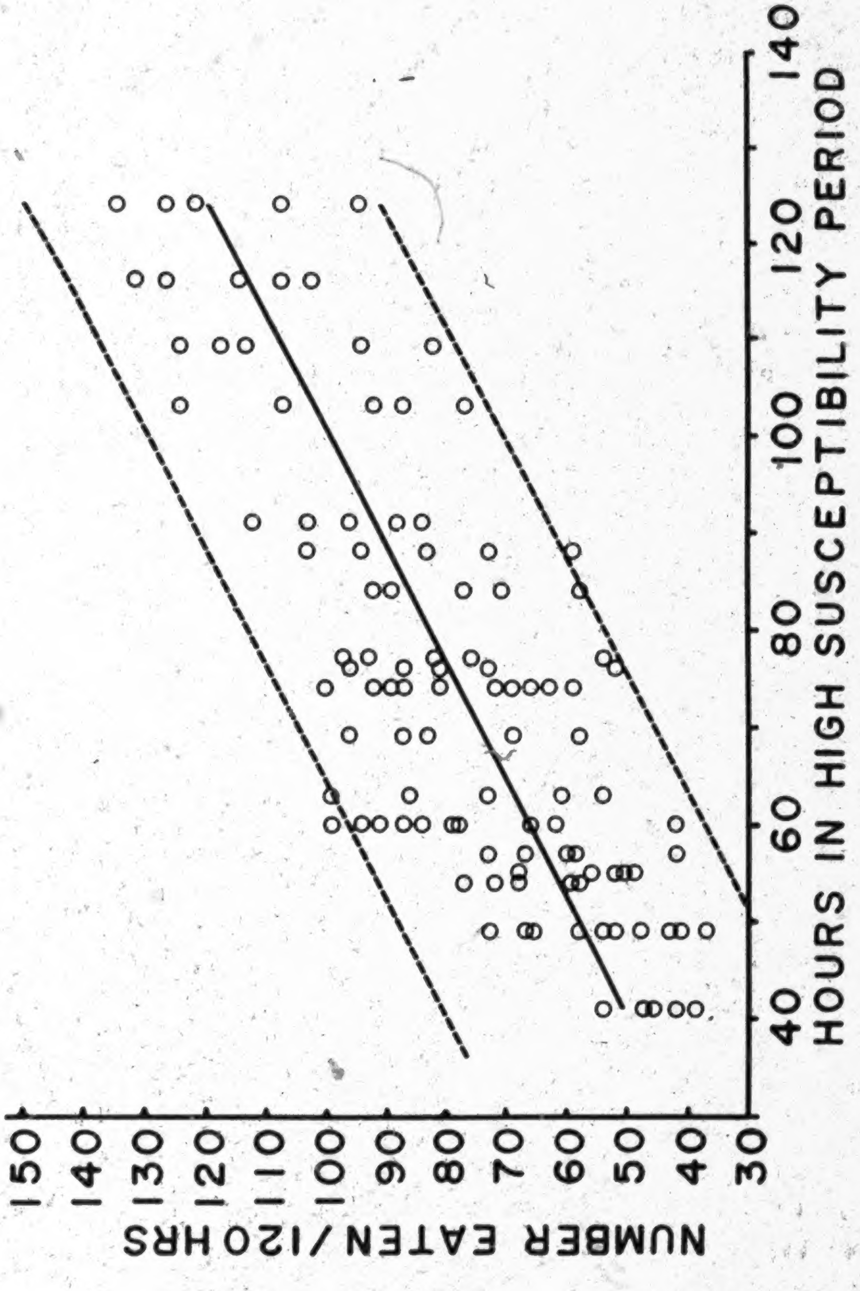

ZOEA PREDATION ON ECHINODERM EMBRYOS (X̄ ± SD)
ECHINOIDS ●
ASTEROIDS ○
CLEARANCE RATE (liters/zoea/day)
.7
.6
.5
.4
.3
.2
9/6
9/10
9/6
9/6
9/6
8
10
12
14
16
TEMPERATURE (°C)

Table 6

Comparison of correlation coefficients for relationships between mortality (# prey consumed/120 hrs), ova volume (10^6 µm^3) and development rate to a feeding larval stage (hrs). Correlation statistics are shown for comparisons made at 12°C and for comparisons made from pooled data collected at 8, 12, and 15°C. Values in parentheses indicate probability levels.

RELATIONSHIP	SAMPLE SIZE	SPEARMAN'S rho	KENDALL'S tau
12°C			
Ova Volume X Dev. Rate	35	0.2143 (0.2115)	0.0476 (0.6721)
Ova Volume X Mortality	35	-0.1366 (0.4257)	-0.1046 (0.3635)
Mortality X Dev. Rate	35	0.4494 (0.0088)	0.3245 (0.0048)
All Temperatures			
Mortality X Dev. Rate	105	0.7623 (<0.001)	0.5902 (<0.001)

Figure 16. Correlation between larval mortality and the duration of the high susceptibility (pre-feeding) period of development. Solid line shows the best fit least-squares regression: $Y = 18.58 + 0.80X$, $r^2 = 0.6195$, $n = 105$. Dashed lines indicate 95% prediction limits above and below the regression line.


NUMBER EATEN/120 HRS
150
140
130
120
110
100
90
80
70
60
50
40
30
HOURS IN HIGH SUSCEPTIBILITY PERIOD
40
60
80
100
120
140

intermediate temperature were used to calculate correlation coefficients (12°C, $p < 0.01$, Table 6). Although the relationship between embryo-larval mortality and development rate is more robust when data from all species and temperatures are considered (Figure 16), the correlation at a single temperature is perhaps more informative because the potentially confounding effects of temperature on zoea metabolic demands are removed. In each case, the number of echinoderm embryos and larvae consumed over a period of 120 hrs was directly proportional to the number of hours necessary for the embryos to develop to the first feeding stage (Table 6, Figure 16). In all species of echinoderms, the early pre-feeding stages were highly susceptible to predation by P. producta in stage-specific feeding experiments (see Figures 10, 13 and 14). Susceptibility to predation by P. producta was consistently lower after larvae began to feed. These results suggest that rapid morphogenesis through the early pre-feeding stages of development may effectively decrease the amount of time spent in the period of high susceptibility to predation by P. producta zoeae.

D. DISCUSSION

The results of this study show that the survival of early embryonic and larval stages of planktotrophic echinoderms are affected in laboratory feeding experiments by the feeding activities of zooplanktonic crustaceans including brachyuran zoeae, Pugettia producta, hyperiid amphipods, Parathemisto pacifica, and mysids, Neomysis rayii. All three crustaceans exhibited similar density-dependent patterns of predation upon embryos of planktotrophic echinoderms. However, there were marked differences in the shapes of stage-specific susceptibility curves between the three predators. These findings suggest that predator-prey interactions between marine invertebrate larvae and carnivorous zooplankton can be complex, and that caution should be exercised in making generalizations about larval mortality patterns from investigations of a few species.

The mortality rates of embryos and larvae of benthic marine invertebrates are generally presumed to be high, but the sources of mortality and dynamics of loss from larval populations are poorly understood (Strathmann, 1985; Hines, 1986). It is likely that adverse hydrographic conditions, failure of larvae to locate an adequate substratum for settlement, and predation upon larvae are major sources of larval mortality. Although laboratory studies of predation upon marine invertebrate larvae cannot directly address rates of embryo and larval mortality in the field, they provide a starting point for the recognition of principles and patterns that emerge from investigations of predator-prey interactions.

In the present study, zoea larvae from Pugettia producta were used as model representatives of carnivorous microcrustaceans. The feeding behavior of brachyuran zoeae has been investigated experimentally by Herrnkind (1968), Sulkin (1978), Incze and Paul (1983), and several others (see Sulkin, 1984, and Rumrill, 1987, for review). In a series of previous papers, Rumrill and Chia (1985), Rumrill _et al_. (1985), and Pennington _et al_. (1986) reported differential rates of predation upon echinoid embryos and larvae by several species of brachyuran zoeae. These previous studies provide evidence that zoeae are raptorial cruising encounter feeders (sensu Greene, 1985) that capture a variety of prey items ranging from phytoplankton to invertebrate embryos and larger zooplankton. The results of the present study are consistent with previous reports of brachyuran feeding behavior and predation rates, and they provide further evidence that brachyuran zoeae may be important predators of marine invertebrate larvae in nearshore waters.

The feeding behavior of hyperiid amphipods has been investigated in the laboratory by Sheader and Evans (1975), von Westernhagen and Rosenthal (1976), and von Westerhagen _et al_. (1979). Their studies show that predatory hyperiid amphipods exhibit a variety of foraging tactics ranging from visual hunting and raptorial feeding to cruising encounter feeding. The high rates of predation upon recently hatched blastulae and prism larvae of _Strongylocentrotus franciscanus_ reported here suggest that _Parathemisto pacifica_ may have used ambush encounter tactics to capture prey in the laboratory predation experiments. Similarly, the feeding behavior of mysids ranges from herbivorous filter-feeding to raptorial carnivory (Mauchline, 1980; Murtaugh, 1981, 1984; Fulton 1982; Mullin and Roman 1986). Murtaugh (1981) reported a tendency for small individuals of *Neomysis mercedis* to select the smallest prey available in laboratory feeding experiments (< 500 µm). In contrast, larger mysids captured and consumed prey items as large as 3 mm in length. In the present study, individuals of *N. rayii* captured small prey items at a high rate compared with capture rates for larger prey in single-stage predation experiments. However, a switch in the feeding response of *N. rayii* occurred when mysids were offered a heterogeneous assemblage of large and small prey items. Observations of *P. pacifica* and *N. rayii* made during feeding in the laboratory suggest that both of these species encounter echinoderm embryos and larvae by chance.

Strongylocentrotid urchins such as *S. franciscanus* and *S. purpuratus* must develop for 50 to 60 hrs (12-15°C) before they are capable of feeding. Similarly, clypeasteroid larvae such as *Dendraster excentricus* develop for 40-45 hrs prior to the onset of feeding. In both types of larvae, the onset of feeding is correlated with a substantial decrease in the susceptibility of larvae to predation by *Pugettia producta*. Similar results have been reported for sea urchin and sand dollar larvae in response to predation by several species of predatory zooplankton (Rumrill _et_ _al_., 1985; Rumrill and Chia, 1985; Pennington _et_ _al_., 1986). Rumrill _et_ _al_. (1985) showed that the decrease in susceptibility of sand dollar echinopluteus larvae was due in part to the development of a post-contact encounter response and the ontogeny of a larval neural system to facilitate large-scale ciliary reversal and backwards swimming.

The implication from benthic marine invertebrate life history studies is that the amount of time spent in embryonic and early larval stages should be minimized to attain maximal numbers of offspring per unit of reproductive effort (Vance, 1973; Caswell, 1981). As a consequence, brood protection and encapsulation of embryos have been suggested as mechanisms to reduce risk during the critical early stages of development (Pechenik, 1979; Grant, 1983; Chaffee and Strathmann, 1984). Results from the present study extend the predictions of life history theory to species with pelagic planktotrophic development. The strong correlation between rates of predation by _Pugettia_ _producta_ and development rates to a feeding larval stage indicate that the time period prior to feeding can be considered as an approximate index of the time spent by the embryo or larvae in a period of high risk.

It must be emphasized, however, that the relationship between mortality and development rate is strongly dependent upon the shape of the stage-specific susceptibility curve determined empirically by investigations of predator-prey interactions. For example, when considering the feeding activities of predatory zooplankton such as brachyuran zoeae, carnivorous copepods, euphausids, and perhaps mysids (Rumrill et al., 1985; Rumrill and Chia, 1985; Pennington et al., 1986), the relatively high susceptibility of embryos and early larval stages yields results similar to those shown in Figure 16. The conclusion from these results would be that a developmental program that includes rapid morphogenesis through the early high susceptibility period should be favored when the frequency of encounters with predatory crustaceans is high. However, opposite results are expected from predatory encounters with planktivorous fish and zooplankton such as hydromedusae and ctenophores that exhibit high rates of predation upon later larval stages (Rumrill, pers. observ.; Pennington et al., 1986). As a consequence, the use of development rate as an index to rank larval susceptibility to predation by carnivorous crustaceans is presently restricted to applications between particular groups of species for which predator-prey interactions have been described empirically. Only limited predictions can be made about the impact of predation for marine invertebrate larvae that have similar morphological traits and comparable rates of development.

It is not yet possible to extrapolate the findings of laboratory investigations of predator-prey interactions between particular species pairs to field situations, although it is likely that predator-prey interactions such as those reported here for Pugettia producta and planktotrophic echinoderms may be similar to interactions with other predatory crustaceans. The importance of predation by zooplanktonic crustaceans in controlling natural populations of echinoderm larvae in nearshore coastal zones is unknown. Mortality rates of larvae due to predation will depend on their rates of encounter with several different types of predators, and with the probability of capture and escape associated with each encounter. Many important aspects of these predator-prey relationships can only be revealed by direct observations of feeding behavior and quantification of stage-specific susceptibilities and the effects of prey density.

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CHAPTER IV.

LOCOMOTION AND PREY CAPTURE BY ZOEA LARVAE OF THE KELP CRAB, *Pugettia producta* (DECAPODA: BRACHYURA: MAJIDAE)

A. INTRODUCTION

The viscosity of seawater plays an important role during locomotion and feeding in several species of herbivorous and raptorial copepods (Ambler and Frost, 1974; Strickler, 1975, 1977, 1982; Alcaraz *et al*., 1980; Koehl and Strickler, 1981; Andrews, 1983). In contrast, comparatively little information is available about the mechanisms of locomotion and feeding for raptorial brachyuran zoeae (Foxon, 1934; Herrnkind, 1968; Schembri, 1982). Detailed descriptions of locomotion and feeding are necessary to determine whether recent generalities concerning feeding hydrodynamics and chemoreception are widespread among raptorial microcrustaceans for capturing food at low Reynolds numbers.

Locomotion and feeding behavior are prominent aspects of the larval biology and ecology of brachyuran zoeae (Forward and Costlow, 1974; Sulkin, 1975, 1984; Cronin and Forward, 1979, 1983; Shanks, 1983). The mechanisms utilized by zoea larvae to swim and capture food are influenced by the functional morphology of their various appendages. As a result, ontogenetic changes in body form have important consequences regarding the diet, growth, and metabolism of zoea and megalopa larval stages. Swimming and feeding behavior are related to several larval traits including mechanisms of zoea depth regulation (Sulkin, 1984), and patterns of onshore larval transport and recruitment (Sulkin et al., 1980; Sulkin and Van Heukelem, 1986; Kelly et al., 1982; Shanks, 1983; Epifanio et al., 1984). Despite the importance of swimming and feeding to the larval ecology of brachyuran zoeae in nearshore coastal waters, only cursory descriptions are available concerning the hydromechanical aspects of locomotion and prey capture (Foxon, 1934; Herrnkind, 1968; Gonor and Gonor, 1973; Lochhead, 1977; Schembri, 1982).

Adult kelp crabs, *Pugettia producta* (Randall, 1839) (Majidae), are herbivorous brachyurans that inhabit canopies of giant kelp (*Macrocystis* spp.) along the west coast of North America (Hines, 1982). Ovigerous females brood continuously throughout the year, and their larvae pass through 2 zoeal stages before molting to the megalopa (Hines, 1982, 1986). In the present study, I describe the mechanisms of swimming and prey capture by *P. producta* zoeae. I use stroboscopic photography to estimate average velocity profiles for unrestrained zoeae during periods of swimming in laboratory aquaria. Flow visualization techniques were used to examine the movements of fluid generated by oscillations of the maxillipeds in tethered zoeae. Information presented here facilitate interpretations of the functional anatomy of brachyuran zoea larvae. Results from this study contribute to the understanding of brachyuran larval behavior and also to the mechanisms utilized by raptorial microcrustaceans to capture prey.

B. MATERIALS AND METHODS

1. Rearing of Larvae

Stage I and II zoeae were raised in culture from ovigerous female crabs. Adult *Pugettia producta* were collected from kelp and wharf-pilings near the vicinity of Bamfield Marine Station, British Columbia (48° 50'N, 125° 08'W) and Friday Harbor Laboratories, Washington (48° 32'N, 122° 59'W). Ovigerous female crabs were held in sea tables until hatching occurred. Stage I zoeae accumulated against a well-lit region of a sea table shortly after release and were placed into 60:L X 30:W X 30:H cm plexiglass aquaria. Seawater in the aquaria was maintained at ambient temperatures (12-13° C) and renewed every second day. Zoeae were exposed to natural photoperiod and were provided with a daily ration of newly hatched brine shrimp nauplii (*Artemia salina*, San Francisco source population).

2. Hydromechanics of Swimming

The swimming behavior of unrestrained and tethered stage I and II zoeae was observed in laboratory aquaria. Stroboscopic photographs were taken of 15 unrestrained zoeae as they swam in a 102:L X 28:W X 80:H mm glass observation chamber. The film plane of the photographic system was focused on the center of the chamber so that zoea which were at a minimal distance of 2-3 body lengths from the nearest glass wall would produce sharply focused images. Critical distances within the photographic system were initially established by shadow triangulation (see Appendix II) and subsequent focal distances were set according to a table of standard zoea body lengths away from the wall of the observation chamber. Stroboscopic illumination was provided within the observation chamber through a narrow slit at 200 and 900 pulses min^{-1} (3.3 and 15 Hz) by a Strobex 236 Stroboscope. The illumination beam was focused in the plane of the observation chamber through a reversed 55 mm Micro-Nikkor lens at f5.6. The lens was equipped with a # 25 red filter and a heat-absorbing shield. Swimming sequences lasting 2-4 s were photographed with Kodak Tri-X film developed at ASA 1600 in Acufine. The swimming velocities of P. producta zoeae were determined by measuring the successive displacement distances between images of zoeae (see Appendix II). Zoeae which made obvious turns or looping trajectories were not included in the analysis. Average swimming velocity and acceleration profiles were found for each zoea by computing the derivatives of fifth-order polynomials fit to measurements of cumulative displacement distances (Lehman, 1977; Hazony, 1979). Since the limits of resolution possible by these techniques are 300 ms (200 pulses min^{-1}) and 67 ms (900 pulses min^{-1}), the average velocity profiles necessarily underestimate instantaneous velocities.

Movements of fluid and the oscillation frequency of swimming appendages were examined for tethered Pugettia producta zoeae in moving water. Zoeae were tethered with cyanoacrylate adhesive to glass needles that had tip diameters approximately half the diameter of the zoea dorsal spine (10-15 µm). A glass needle was affixed to each zoea at a point along the posterior margin of the dorsal spine about 50 - 100 µm above the carapace (see Figure 24a). Although placement of a glass needle in this position caused an eddy to form immediately downstream of the tethered zoea in a flow tank (Figure 27a), glass needles placed in other positions resulted in greater disruption of currents around the zoea maxillipeds. Tethered zoeae were positioned about 20-22 body lengths away from the walls of a rectangular plexiglass container (400:L X 50:W X 50:H mm) filled with 0.45 µm filtered seawater. The container was mounted on a set of 16 low-friction wheels and pulled along a 1 m track. Force was applied to the container through nylon strings wound around an electrically powered rotating shaft. The flowtank was capable of moving filtered seawater past the tethered zoeae at velocities between 0.6 and 3.7 mm s^{-1}.

Swimming currents generated by the 1st and 2nd maxillipeds of Pugettia producta were examined by photography of dye streamlines. Seawater dyed with 1% aniline blue was released from a micropipette positioned upstream from the tethered zoea and photographed as it moved past the carapace and swimming appendages. Oscillation frequencies and velocities of the swimming and feeding appendages were determined by observing the movements of tethered zoeae while they were illuminated with stroboscopic light. The frequency of oscillation was determined for 12 zoeae by adjusting the stroboscope to freeze the motion of the maxillipeds. Appendage velocities were determined from measurements of the distance traveled by the appendage during effective strokes.

3. Hydromechanics of Particle Capture

Sequential photographs were taken to form a composite record of the feeding events that occurred while tethered zoeae captured and consumed non-motile and motile prey items. Prey items in these observations were freshly excised oocytes, embryos, and gastrula larvae from the sea star, *Patiria miniata*. Prey items moved past the tethered zoeae at a velocity of 1.2 mm s^{-1} in the flowtank. The concentration of prey items in the flowtank was between 5-12 prey ml^{-1}.

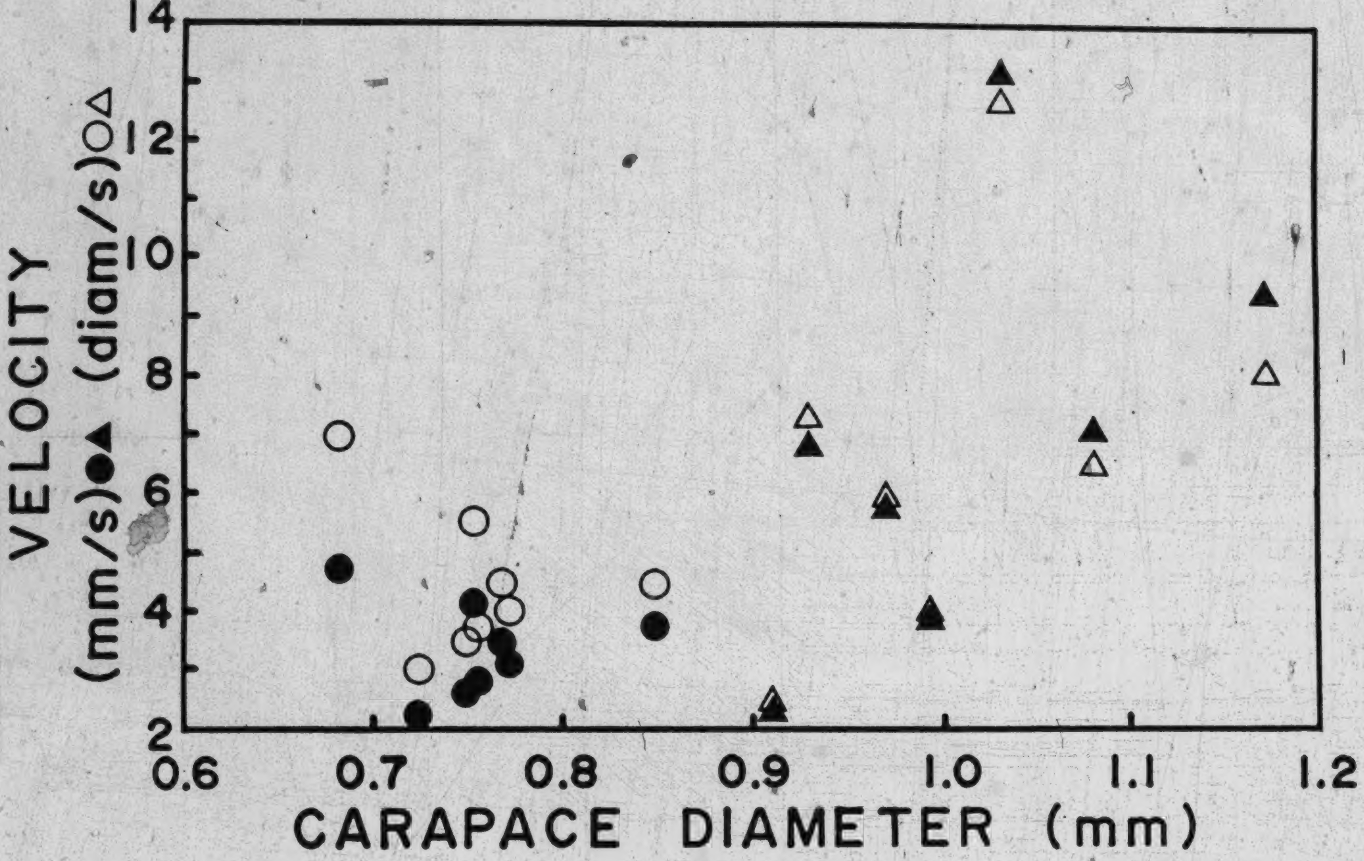
C. RESULTS

1. Swimming Behavior of *Pugettia producta* zoeae

The swimming behavior of *Pugettia producta* zoeae in laboratory aquaria was characterized by jerky or pulsed motion. During periods of oriented swimming, zoeae exhibited frequent periods of acceleration as they propelled themselves in the direction of the dorsal spine. When beating of the maxillipeds ceased, the zoeae rolled anteriorly and sank at 2 to 3 mm s^{-1}. In general, the swimming behavior of P. producta was similar to the gliding motion of calanoid copepods (see Strickler, 1975), although P. producta zoeae often swam with intermittent changes in velocity for 4 to 5 s before changing direction.

Figure 17 shows the relationship between carapace diameter and mean swimming velocity standardized over a period of 3 seconds. Absolute velocities and relative velocities showed similar relationships with increasing zoea carapace diameter. Stage I zoeae of P. producta had an average carapace diameter of 756±47 µm and a mean swimming velocity of 3.3±0.8 mm s^{-1}. By comparison, stage II zoeae had significantly larger carapace diameters (1012±91 µm; $t = 6.99$, $p < 0.001$) and greater swimming velocities (7.4±3.8 mm s^{-1}; $t = 2.92$, $p = 0.012$). The relative velocities reached by stage I zoeae averaged 4.4±1.3 body lengths s^{-1} compared to 6.7±3.3 body lengths s^{-1} for stage II zoeae. The relationship between absolute swimming velocity and carapace diameter was best fit by an exponential least-squares regression equation ($Y = 6.19X^{2.22}$); $r^2 = 0.4899$, $p = 0.004$). The value of the exponent suggests that the faster swimming speeds of stage II zoeae may be directly related to ontogenetic

Figure 17. The relationship between swimming velocity and carapace diameter for stage I and stage II zoea larvae of Pugettia producta. Absolute velocities (mm s^{-1}) of stage I (●) and stage II (▲) zoeae are related to carapace diameter by $Y = 6.19X^{2.22}$, $r^2 = 0.4899$, $p = 0.004$. Relative velocities (carapace diameters s^{-1}) of stage I (○) and stage II (△) zoeae are related to carapace diameter by $Y = -2.37 + 8.98\ X$, $r^2 = 0.2634$, $p = 0.050$.


VELOCITY
(mm/s)●▲ (diam/s)○△
14
12
10
8
6
4
2
0.6
0.7
0.8
0.9
1.0
1.1
1.2
CARAPACE DIAMETER (mm)

changes in the surface area of the maxilliped propulsion system and the distribution of drag forces along the carapace (Table 7, Figure 24).

2. Velocity and Acceleration Profiles

Time-series analysis of stroboscopic photographs showed that each individual *Pugettia producta* zoea exhibited a unique average velocity profile (Figures 18-22). Average velocity profiles obtained from stroboscopic photographs with resolutions of 300 and 67 ms cannot be used to accurately determine instantaneous acceleration values because changes in the velocity of microcrustaceans can occur over much shorter periods of time (see Strickler, 1975; Lehman, 1977). Nevertheless, the average velocities shown in Figures 18-22 provide a first approximation of the locomotory behavior of unrestrained *P. producta* zoeae, and they can serve as minimal estimates of acceleration during changes in zoea swimming velocity.

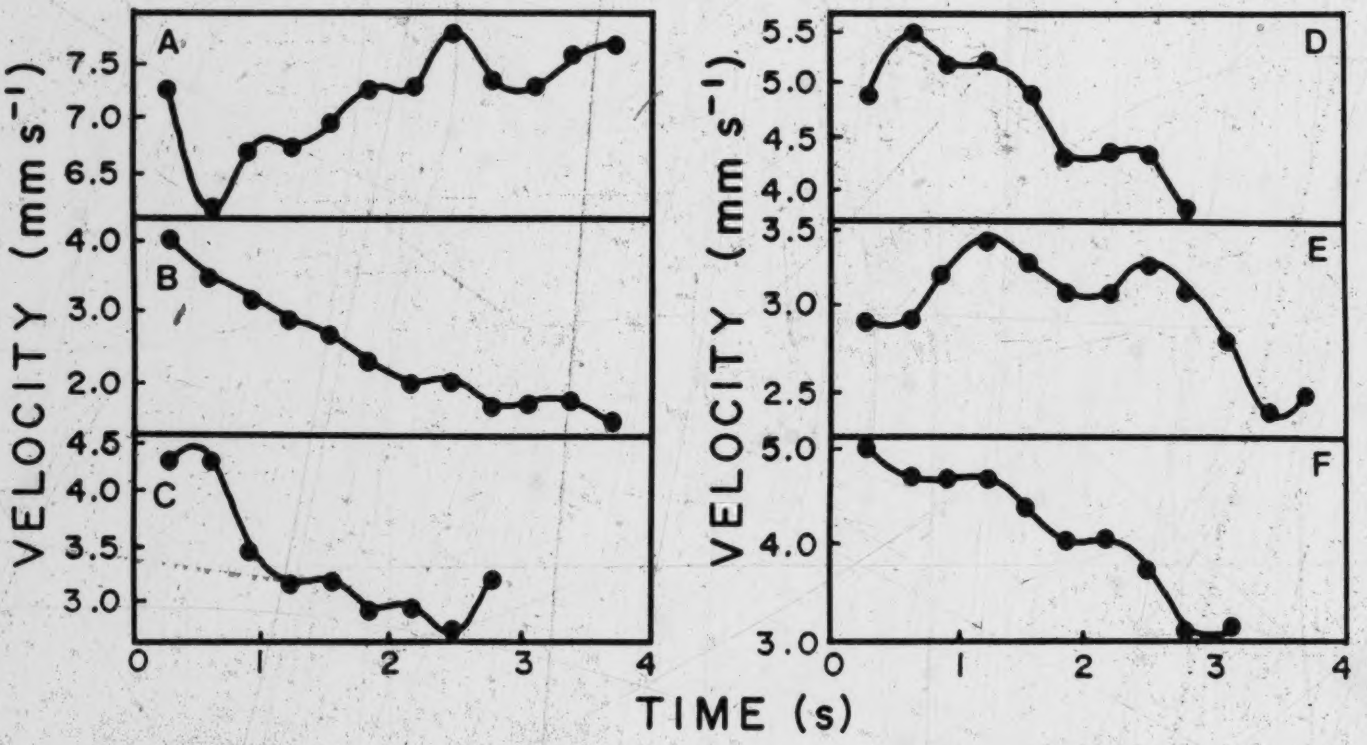
Average swimming velocity profiles are presented graphically for 6 unrestrained *Pugettia producta* stage I zoeae in Figure 18a-f. The first zoea showed a net increase in velocity over the 3.7 s observation period (Figure 18a). The increase in velocity occurred following 4 periods of net acceleration and 2 periods of net deceleration. Similar average velocity profiles were observed for other stage I zoeae. For example, 4 of the zoeae exhibited a net decrease in swimming velocity over the 3 or 4 s observation periods (Figures 18b-d, f). In each case, the overall decrease in

TABLE 7

Comparison of morphological features between stage I and stage II zoea larvae of *Pugettia producta*. Table entries show mean (± s.d.). All units are micrometers unless indicated otherwise.

	SAMPLE SIZE	STAGE I		STAGE II		COMPARISON	
	Stage I/II	Mean	(s.d.)	Mean	(s.d.)	t test	p
Carapace	35/24						
Diameter		801.1	(44.1)	1043.4	(71.5)	16.10	<0.001
Projected Surface Area μm^2		5.1×10^5	(0.5)	8.6×10^5	(1.2)	15.57	<0.001
1st Maxilliped	19/17						
# of Setae		4		6			
Seta Length		323.3	(10.8)	341.2	(11.0)	4.90	<0.001
2nd Maxilliped	19/17						
# of Setae		4		6			
Seta Length		384.8	(22.8)	364.5	(17.7)	2.94	0.006
Surface Area of Natatory Setal Field μm^2	19/17	7.3×10^4	(0.4)	8.2×10^4	(0.4)	6.41	<0.001
Telson	19/17						
Length		758.9	(52.8)	960.9	(49.1)	11.83	<0.001
Width		556.3	(49.7)	805.3	(36.6)	16.94	<0.001
Velocity mm/s	8/7	3.3	(0.8)	7.4	(3.8)	2.92	0.012
Relative Velocity mm/s	8/7	4.4	(1.3)	6.7	(3.3)	1.77	0.099

Figure 18. Velocity profiles for 6 stage I zoea larvae of Pugettia producta. Data points show successive swimming velocities calculated from displacement distances on photographs taken with stroboscopic illumination at 200 flashes min^{-1}. Each point shows swimming velocity averaged over a period of 300 ms. Lines show fifth-order polynomials fit to successive velocities.

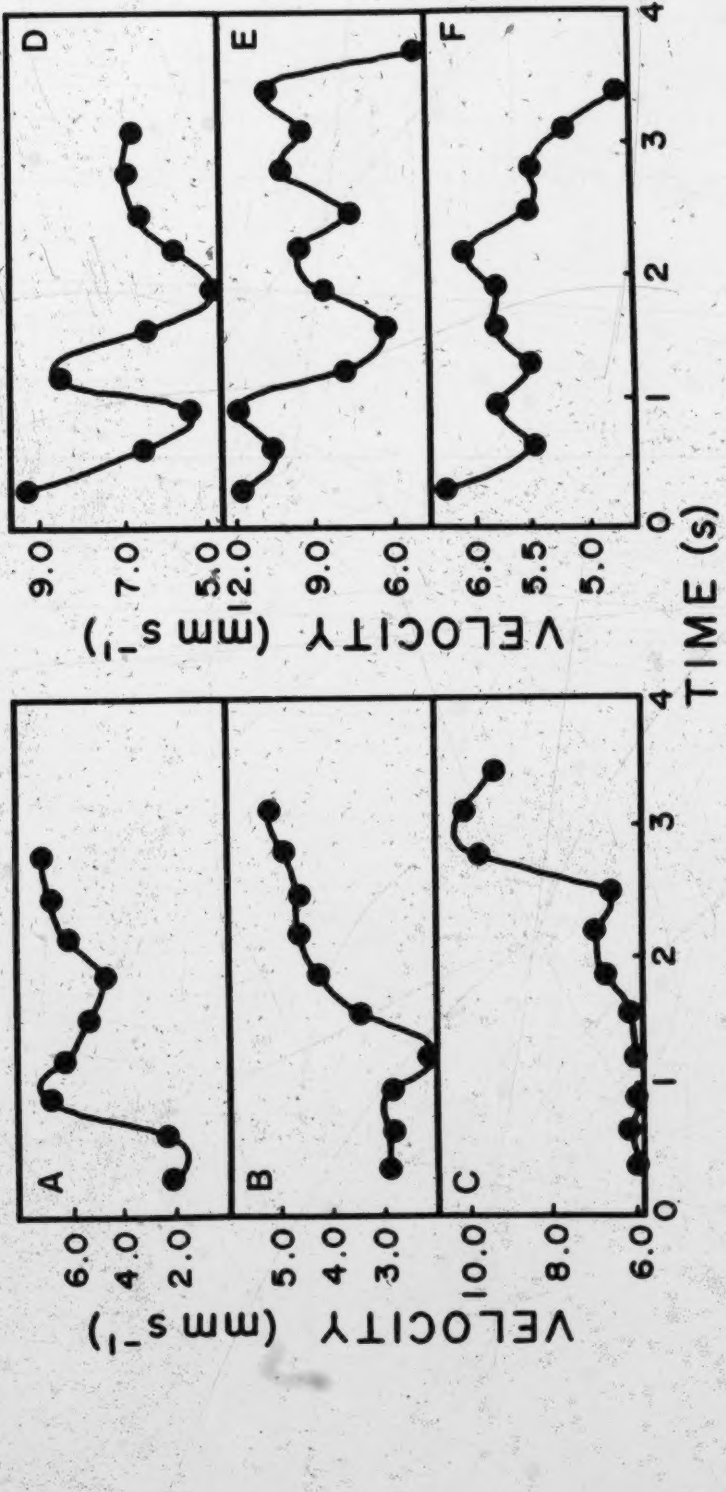

A
B
C
D
E
F
VELOCITY (mm s⁻¹)
7.5
7.0
6.5
4.0
3.0
2.0
4.5
4.0
3.5
3.0
VELOCITY (mm s⁻¹)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
5.0
4.0
3.0
0
1
2
3
4
TIME (s)

swimming velocity occurred after a series of 3 periods of net deceleration. The final stage I zoea showed cyclic changes in swimming velocities between 2.4 and 3.4 mm s^{-1} over a period of 3.1 s, and exhibited 3 periods of net acceleration and 2 periods of net deceleration (Figure 18e). The temporal changes in swimming speed shown by these average velocity profiles provide an indication that the swimming velocity of P. producta zoeae can fluctuate substantially over periods of 3-4 s.

Average velocity profiles for stage II zoeae are shown in Figure 19a-f. Three of the zoeae exhibited net increases in swimming velocity (Figure 19a-c). Each zoea underwent 2 or 3 periods of net acceleration, and their swimming velocities reached 6.9, 5.4, and 9.9 mm s^{-1}, respectively. The average velocity profiles for the remaining stage II zoeae of Pugettia producta exhibited more complex kinematics characterized by several periods of net acceleration and deceleration (Figure 19d-f). During the 4 s observation periods, the swimming velocities changed in a sinusoidal manner with 2-4 periods of net acceleration and 3-5 periods of net deceleration. The greatest speeds reached by these zoeae were 9.2, 12.1 and 6.4 mm s^{-1}, respectively.

Velocity profiles obtained for 3 stage I zoeae from stroboscopic photographs taken at 900 pulses min^{-1} provide a more detailed record of changes in swimming speed (Figures 20-22). Like the previous velocity profiles, the

Figure 19. Velocity profiles for 6 stage II zoea larvae of *Pugettia producta*. Data points show successive swimming velocities calculated from displacement distances on photographs taken with stroboscopic illumination at 200 flashes min^{-1}. Each point shows swimming velocity averaged over a period of 300 ms. Lines show fifth-order polynomials fit to successive velocities.


A
B
C
D
E
F
VELOCITY (mm s⁻¹)
VELOCITY (mm s⁻¹)
6.0
4.0
2.0
5.0
4.0
3.0
10.0
8.0
6.0
9.0
7.0
5.0
12.0
9.0
6.0
6.0
5.5
5.0
0
1
2
3
4
TIME (s)

zoeae shown in Figures 20-22 also exhibited marked fluctuations in their absolute swimming speeds. The first zoea showed a net increase in swimming speed from 1.6 to 3.1 mm s^{-1} over a period of 2.5 s (Figure 20). During the observation period the zoea alternated between positive and negative acceleration values, and changes in velocity occurred at a frequency 4.5 Hz. The remaining zoeae also exhibited sinusoidal changes in velocity and acceleration (Figures 21 and 22) that were typical of the jerky locomotory behavior observed previously for other zoeae (see Figures 18-20). These results indicate that changes in swimming velocity can occur over periods of 67 ms or less, and that zoeae are capable of accelerating at rates approaching 20 mm s^{-2}.

Although the absolute and relative swimming velocities of Pugettia producta stage II zoeae were greater than those of stage I zoeae (Figure 17, Table 7), the general pattern of locomotory behavior did not change between molts (Figures 18-19). In all cases, zoeae increased or decreased their swimming velocities over short periods of time. Periods of constant speed were limited to about 140 ms by the resolution of the photographic recording system. Rapid fluctuations in velocity and acceleration indicate that the swimming of P. producta zoeae may be incompatible with steady-state hydrodynamics. Furthermore, they suggest that added-mass forces generated during periods of acceleration and deceleration may be an important component of the total

Figure 20. Instantaneous velocity and acceleration profile for a stage I zoea larva of *Pugettia producta*. Data points show successive swimming velocities and acceleration rates calculated from displacement distances on photographs taken with stroboscopic illumination at 900 flashes min^{-1}. Each point shows swimming velocity and acceleration averaged over a period of 67 ms. Lines show fifth-order polynomials fit to successive velocity and acceleration values.

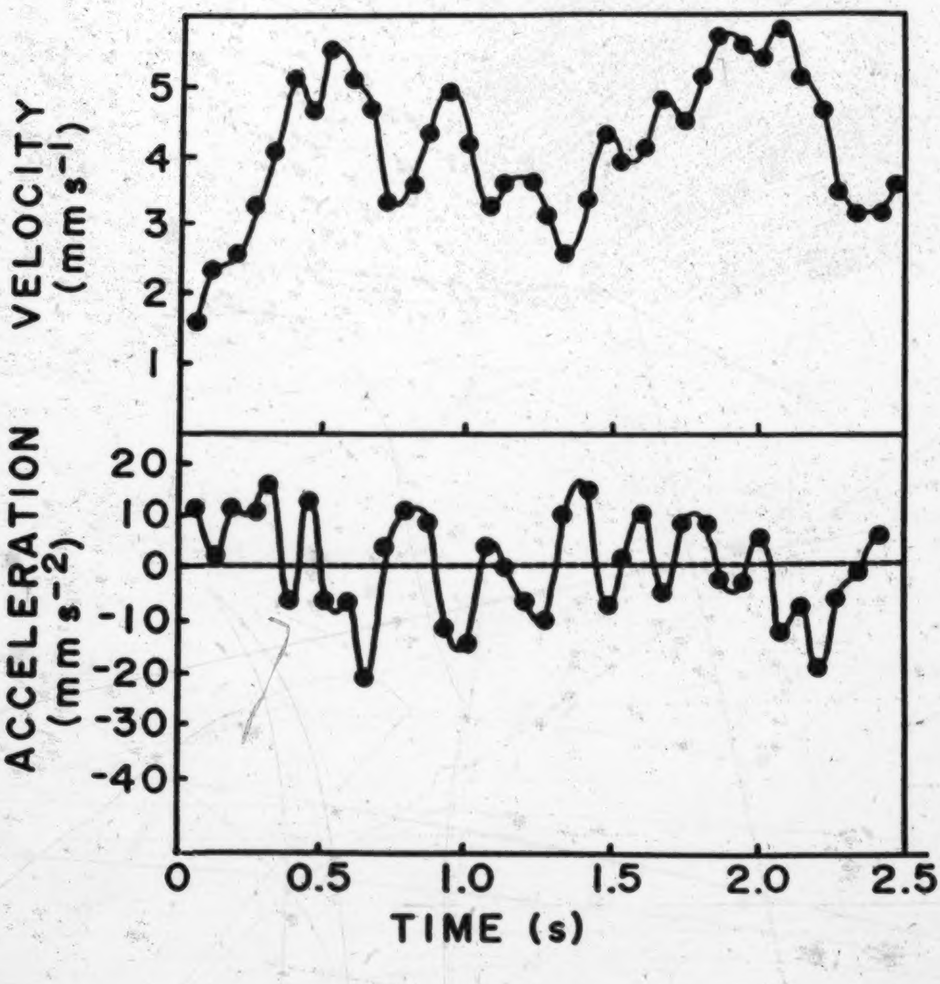

VELOCITY (mm s⁻¹)
5
4
3
2
1
ACCELERATION (mm s⁻²)
20
10
0
-10
-20
-30
-40
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

Figure 21. Instantaneous velocity and acceleration profile for a stage I zoea larva of *Pugettia producta*. See Figure 20 for explanation.

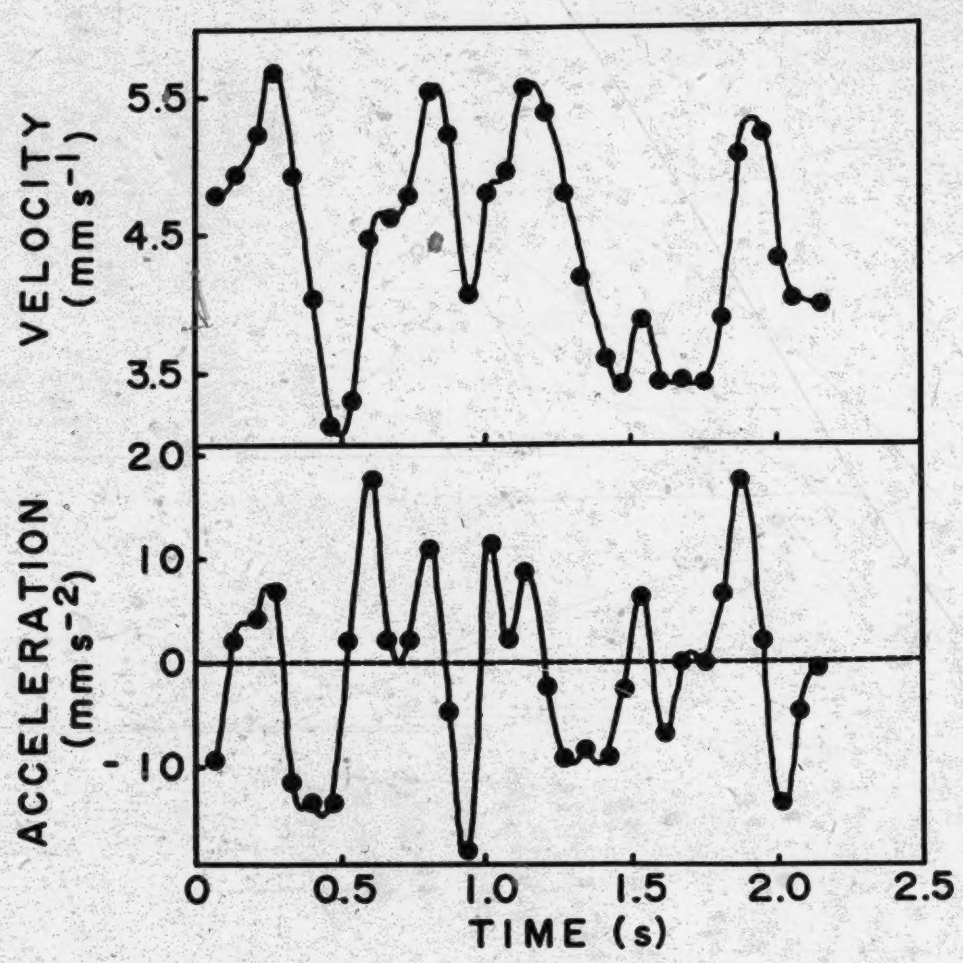
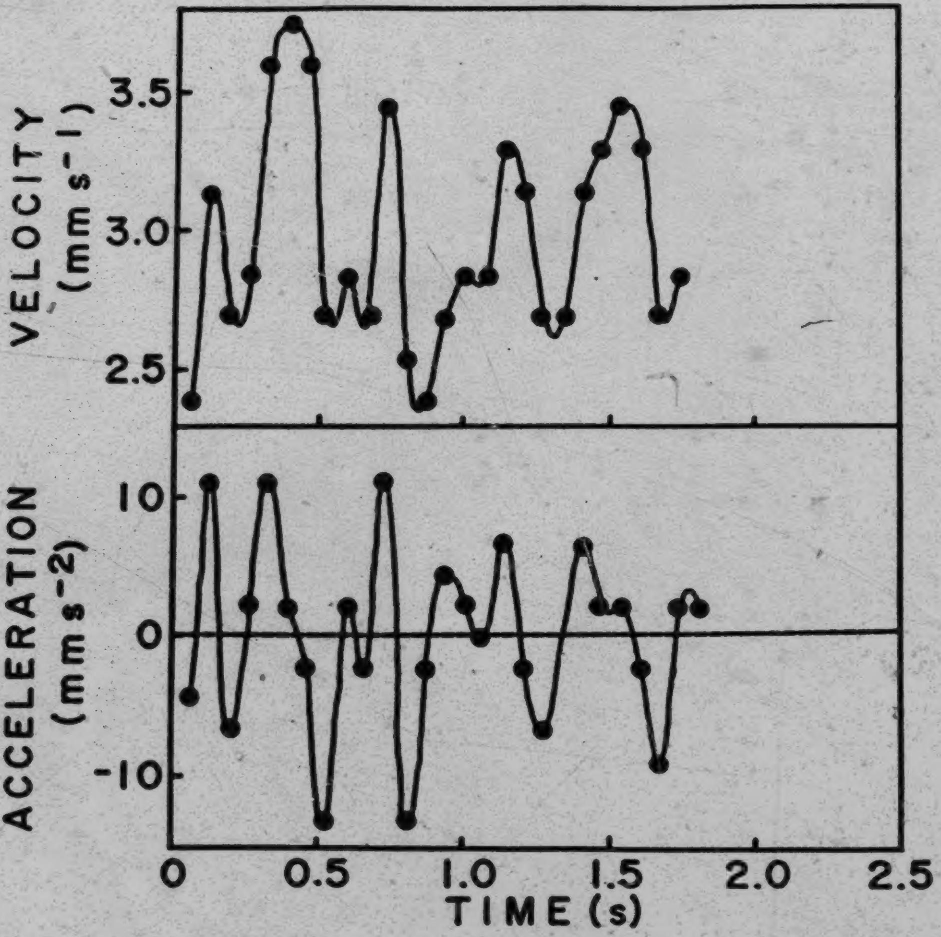

VELOCITY (mm s^{-1})
5.5
4.5
3.5
ACCELERATION (mm s^{-2})
20
10
0
-10
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

Figure 22. Instantaneous velocity and acceleration profile for a stage I zoea larva of Pugettia producta. See Figure 20 for explanation.


VELOCITY (mm s^{-1})
3.5
3.0
2.5
ACCELERATION (mm s^{-2})
10
0
-10
0
0.5
1.0
1.5
2.0
2.5
TIME (s)

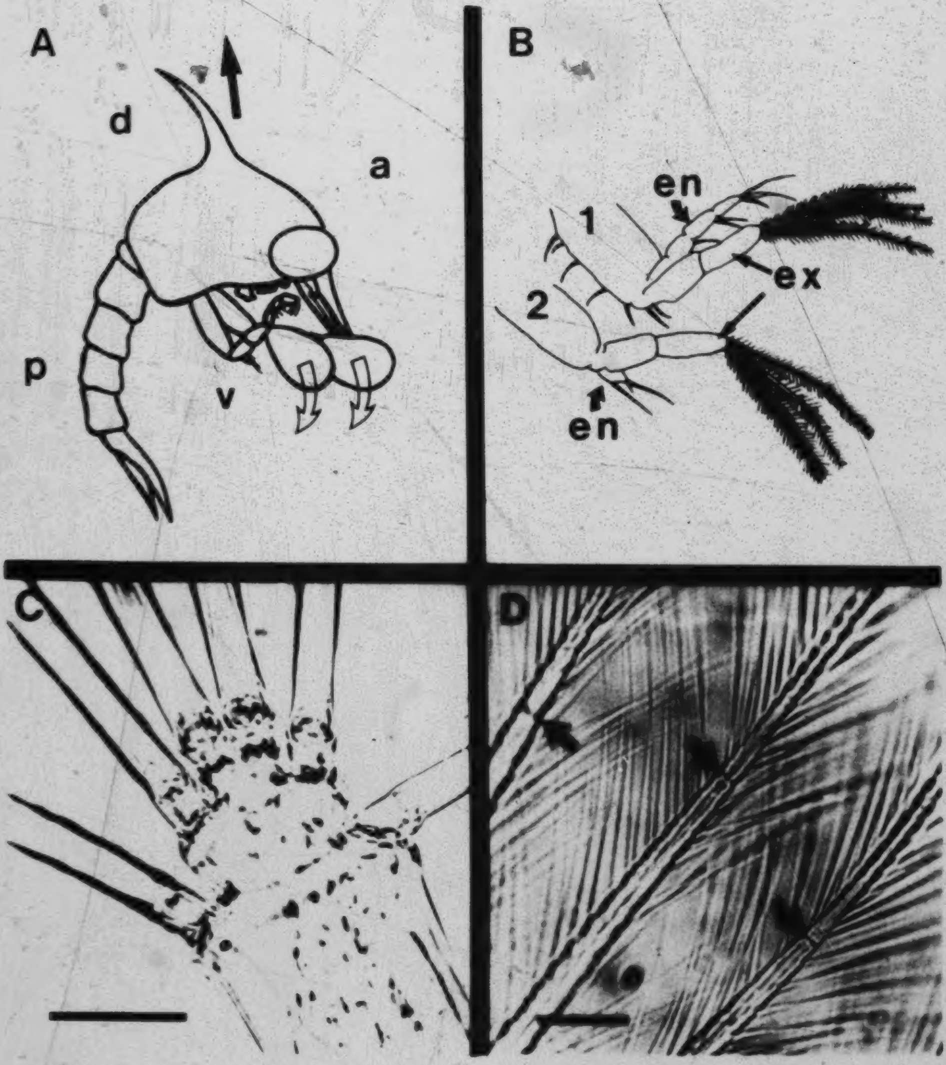
drag forces that resist the motion of a P. producta zoea during locomotion.

3. Morphology of the Swimming and Feeding Appendages

Table 7 shows the ontogenetic changes in body size and other morphological traits that occur during the molt from stage I to stage II in zoea larvae of Pugettia producta. The zoea carapace increases substantially in diameter and projected surface area, and the number of natatory setae on the 1st and 2nd maxillipeds increases from 4 to 6. Although the 1st maxilliped natatory setae increase in length, those of the 2nd maxilliped decrease in length. Nevertheless, the projected surface area of the natatory setal field increases by 12% between molts (Table 7).

Zoea larvae of Pugettia producta generate propulsive forces by rapid oscillations of the 1st and 2nd maxillipeds (Figure 23a). The 1st and 2nd maxillipeds of P. producta are biramous appendages, and each appendage is composed of an endopodite and an exopodite (Figure 23b). Exopodites give rise to 4 natatory setae in the stage I zoea and to 6 natatory setae in the stage II zoea (Table 7, Figure 23c). The natatory setae project distally from the exopodite in the shape of a paddle or fan (Figures 23a, 24c). The natatory setae are plumose and give rise to setules that project laterally to form a lattice throughout the setal field (Figure 23d). Cuticular joints are located 2/3 and 3/4 of the distance along the length of each natatory seta (Figure 23d). In addition, basal joints are located at the

Figure 23. Morphological traits of *Pugettia producta* zoeae. A. Diagram of general zoea body plan. a=anterior, p=posterior, d=dorsal, v=ventral. Open arrows show direction of 1st and 2nd maxilliped effective strokes. Solid arrow shows direction of locomotion during normal swimming. B. Maxillipeds from stage I zoea. 1=1st maxilliped, 2=2nd maxilliped, en=endopodite, ex=exopodite. C. Basal joints on maxilliped of a stage II zoea. Scale bar = 25 µm. D. Natatory setal field and lattice of setules. Arrows show articulating joints on natatory setae. Scale bar = 25 µm.


A
d
a
p
v
B
en
1
ex
2
en
C
D

point where the natatory setae originate from the exopodite (Figure 23c), and at the base of each setule (Figure 23d).

The Reynolds number, Re, a measure of the relative effects of fluid inertia and viscosity, was computed as

$$Re = p\ U\ L\ /\ u$$

where p and u are the density (1.025×10^3 kg m^{-3}) and dynamic viscosity of seawater (1.1×10^{-3} kg m^{-1} s^{-1}; 15° C, salinity 33 ppt), U is the maximum observed velocity of the zoea or appendage, and L is a linear measurement of the zoea carapace or appendage. Re values were above unity for unrestrained stage I and II zoeae (Table 8) and indicate that non-reversible flows and inertial forces are an important aspect of zoea locomotion when considered at the level of the entire zoea body. Since Re values are scaled to the product of length and velocity, they were inherently correlated with zoea body size and molt ($Y = 6.04X^{4.01}$, $r^2 = 0.75$, $p < 0.001$). Lower Re values (10^{-1} - 10^{-2}) are associated with the telson and various components of the 1st maxilliped (Table 8). These low Re values indicate that fluid motion is governed by the effects of viscosity within boundary layers surrounding the swimming appendages and feeding structures.

4. Hydromechanics of Swimming

Visualization of fluid movements with dye-marked water showed that tethered zoea propel seawater past themselves

TABLE 8

Comparison of linear dimensions, velocities, and Reynolds numbers for zoea larvae and various appendages. Table entries show mean (± s.d.). Linear dimension for Reynolds numbers are indicated by brackets.

	SAMPLE SIZE	LINEAR DIMENSION (µm)	VELOCITY (mm/s)	REYNOLDS NUMBER
Carapace	15	875.64	5.24	4.57
[diameter]		(148.87)	(2.69)	(2.64)
Telson Spine	15	585.67	8.09	0.44
[diameter]		(6.19)	(1.09)	(0.06)
1st Maxilliped				
Exopodite Tip	8	30.85	16.73	0.48
[width]		(2.77)	(3.02)	(0.08)
Natatory Seta	8	6.25	18.14	0.10
[diameter]		(0.71)	(2.67)	(0.02)
Natatory Setule	7	1.92	22.62	0.02
[diameter]		(0.56)	(2.60)	(0.002)
Endopodite Tip	8	30.52	1.36	0.04
[width]		(2.67)	(0.32)	(0.01)

by rapid oscillations of their 1st and 2nd maxillipeds (Figure 24). Observations made with a stroboscope indicate that the maxillipeds oscillate at frequencies between 21 and 34 Hz. Propulsive forces are generated in the ventral direction by effective strokes of the maxillipeds. Drag forces are reduced during recovery strokes by decreasing the projected surface area of the natatory setal field.

Laboratory observations of tethered Pugettia producta and other unidentified brachyuran zoeae showed that the following events take place during a typical effective-recovery stroke cycle. Moving fluid first contacts the dorsal surface of the carapace (Figure 24a). Fluid is sheared past the lateral margins of the carapace by sweeping movements of the paired maxillipeds. At the end of the effective stroke, fluid is propelled in the ventro-lateral direction away from the central mass of the zoea body (Figure 23a, 24a). Fluid shed by the tips of the natatory setae gives rise to a pair of toroidal vortices (Figure 24b). The vortex radii increase rapidly as the velocity of the swimming current decreases to ambient levels at a distance 3-4 body lengths away from the tethered zoea.

A diagrammatic summary of the effective and recovery stroke cycle is shown in Figure 25. At the beginning of the effective stroke the maxillipeds and natatory setae extend dorso-laterally at a positive angle of approximately 40-45 degrees (Figures 25 and 26). During the effective stroke,

Figure 24. Movements of fluid and maxillipeds by tethered zoeae. A. Visualization of swimming currents generated by a tethered zoea in a flow tank. The zoea is restrained by a glass needle. Dye released upstream from the zoea was propelled ventrally by rapid beating of the maxillipeds. Solid arrow shows direction of flow tank current (1.2 mm s^{-1}). B. Unidentified brachyuran zoea collected from the plankton. Dye shows toroidal vortex shed by the maxilliped at the end of the effective stroke. C. Natatory setae of the 2nd maxilliped at the end of an effective stroke. Arrows show distance between marginal natatory setae and illustrate large projected surface area of natatory setal field. D. Alignment of the natatory setae at the beginning of the recovery stroke. Arrows show distance between marginal natatory setae and illustrate decrease in projected surface area of the natatory setal field. Scale bars in C and D are 100 µm.

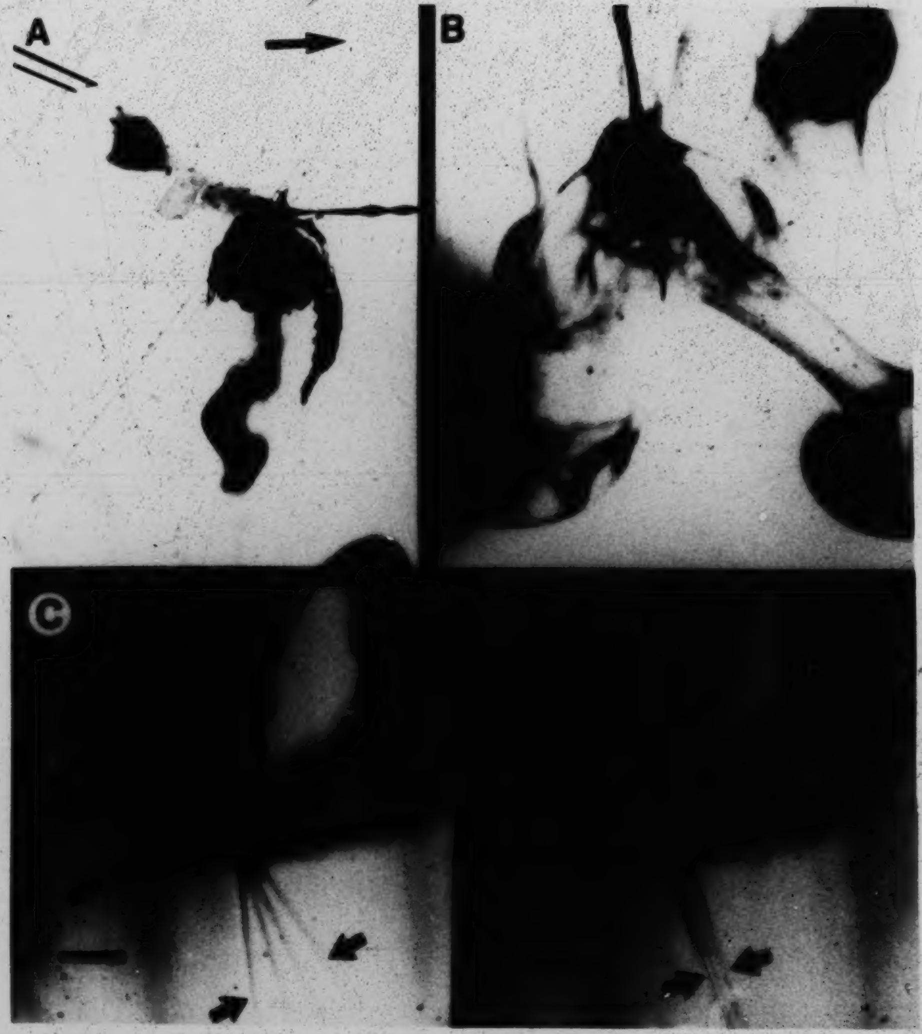

A
B
C

Figure 25. Diagrammatic summary of the oscillation cycle of the 1st and 2nd maxillipeds. Solid appendage and solid arrow indicates 1st maxilliped. Open appendage and open arrow indicates 2nd maxilliped. Oscillation frequencies range from 21 to 34 Hz.

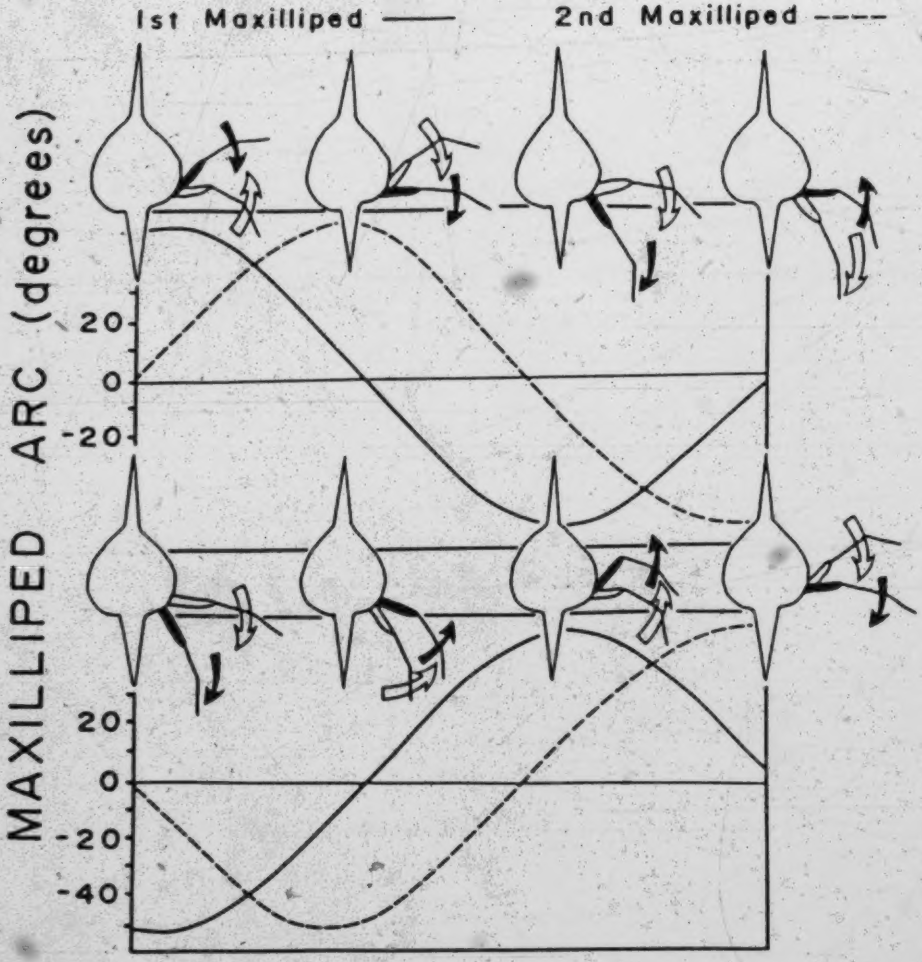
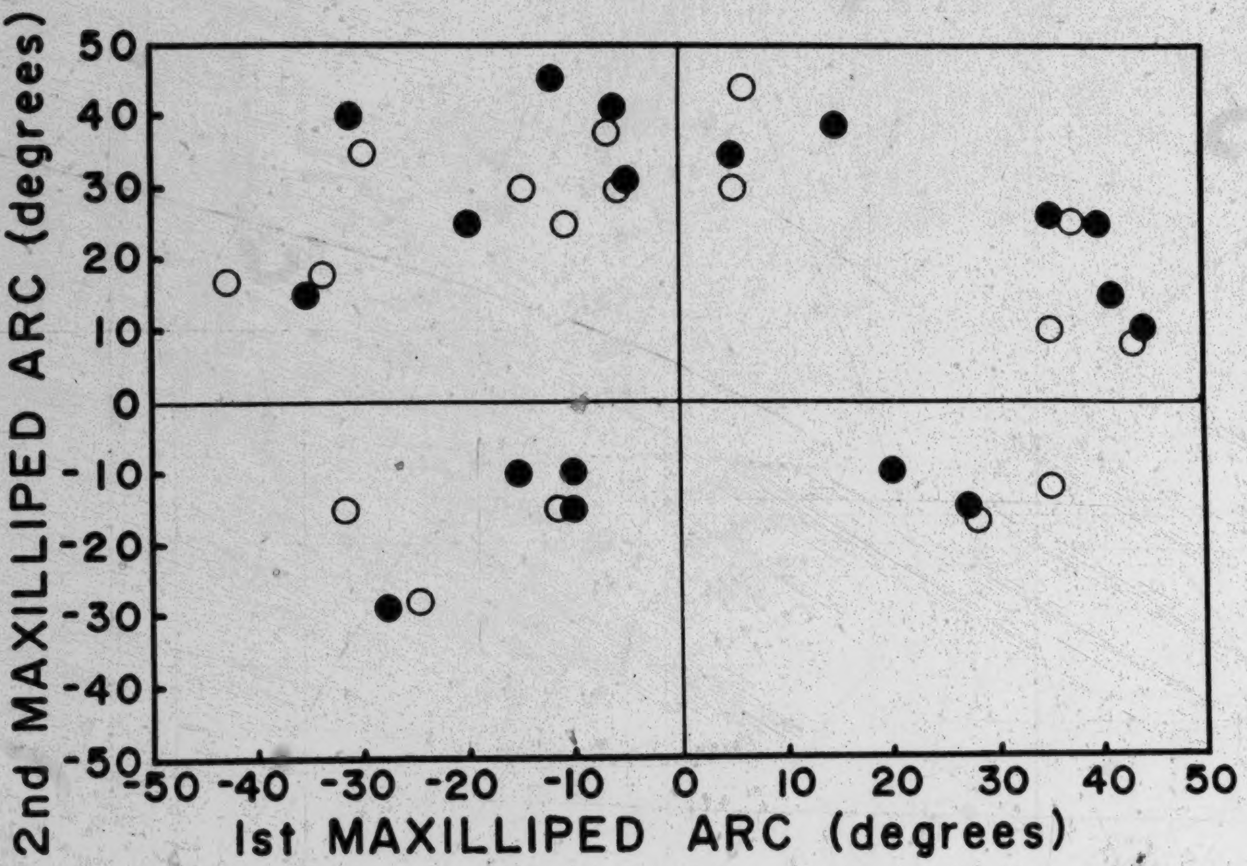

1st Maxilliped ——
2nd Maxilliped ----
MAXILLIPED ARC (degrees)
20
0
-20
20
0
-20
-40

Figure 26. Relationship between the effective and recovery stroke cycles of the 1st and 2nd maxillipeds of a *Pugettia producta* stage I zoea. Each point shows the angles of the appendages measured from a series of 18 flash photographs. Solid circles (●) indicate right side of zoea body, open circles (○) indicate left side. Stroke cycle proceeds counter-clockwise with effective stroke across the top of the plot and recovery stroke across the bottom. Positive arc angles indicate dorso-lateral orientation, negative values indicate ventro-lateral orientation.


2nd MAXILLIPED ARC (degrees)
50
40
30
20
10
0
-10
-20
-30
-40
-50
-50
-40
-30
-20
-10
0
10
20
30
40
50
1st MAXILLIPED ARC (degrees)

the natatory setae shear fluid along the dorsal surface of the carapace and sweep it past the body. The natatory setae project laterally from the maxillipeds during the effective stroke with a chord approximately normal to the plane of fluid motion. The tips of the natatory setae describe an arc of 85-95 degrees over the entire effective stroke. At the end of the effective stroke, the maxillipeds and natatory setae project ventro-laterally at a negative angle of 40-50 degrees (Figures 25 and 26).

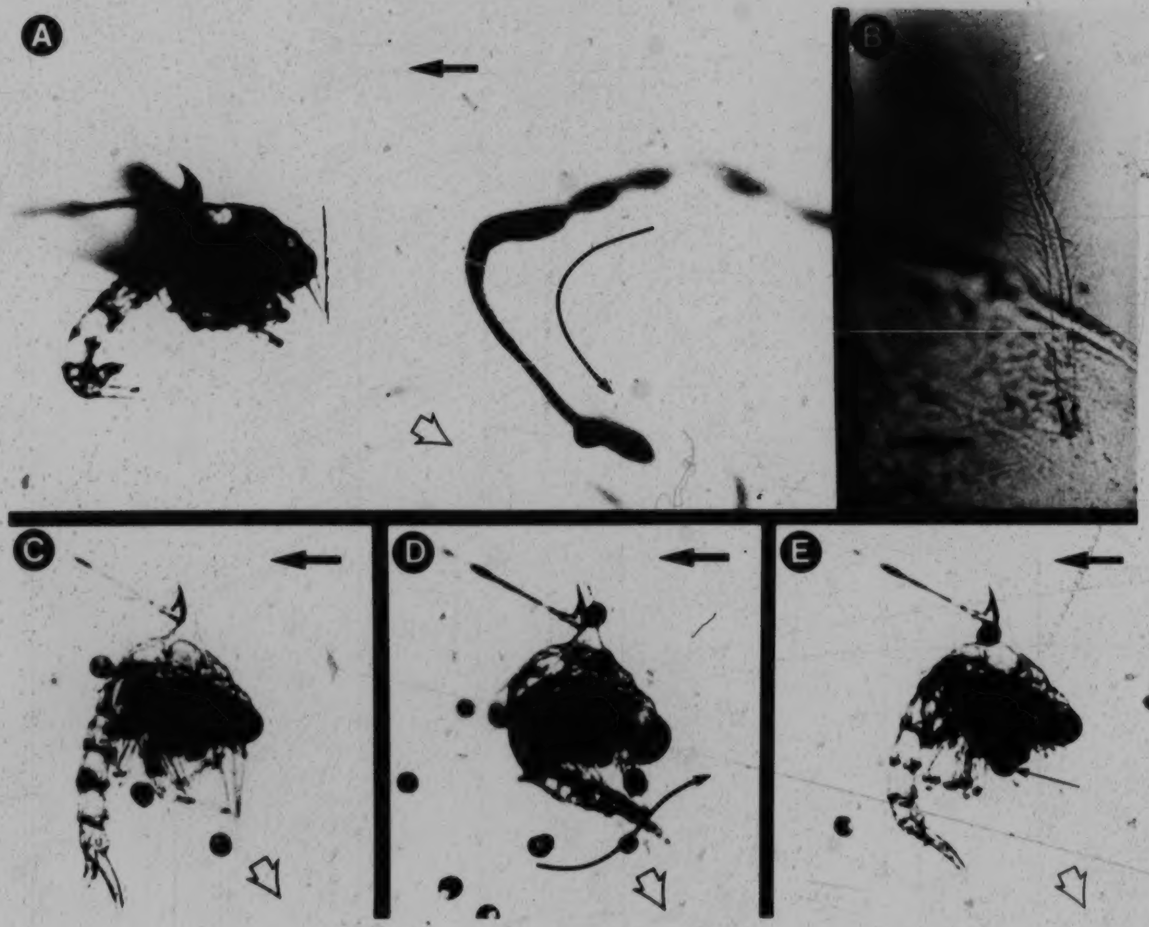
Two different mechanisms are utilized to reduce drag on the natatory setal field during the recovery stroke. First, at the initiation of the recovery stroke the natatory setae are oriented nearly parallel to one another (Figure 24d). Alignment of the natatory setae decreases the basal angle of the setal fan from about 32 to 9 $^{\circ}$, thereby reducing the projected surface area of the 2nd maxilliped setal field by 71%. Second, deformation of the natatory setae and setules along the series of cuticular joints results in a further reduction of the projected surface area of the setal field (Figure 23c,d). Rotation of the setal fan out of the plane perpendicular to flow (pronation) does not appear to be utilized to reduce drag during recovery strokes. At the end of the recovery stroke, the maxillipeds and natatory setae return to their starting position and project dorso-laterally at a positive angle of 45-50 degrees (Figures 25 and 26). The stroke cycle of the 1st maxilliped is generally 80-100 degrees out-of-phase with the stroke cycle of the 2nd maxilliped. However, several photographs of tethered zoeae recorded periods when the maxillipeds were beating in-phase at the end of effective strokes.

5. Capture of Prey Items

During normal swimming of *Pugettia producta* zoeae, dye-marked water does not enter the region immediately surrounding the mouthparts (Figure 27a). During capture of small non-motile prey items, however, seawater is redirected toward the maxillae and mouth by a sweeping effective stroke of the abdomen and telson. Events that occur during the capture of *Patiria miniata* oocytes by a tethered *P. producta* zoea are summarized in Figure 27c-e.

Prior to the onset of the feeding response, the abdomen and telson are extended beneath the carapace and fluid movement past the zoea is predominantly in the ventral direction (Figures 24a and 27c). During the effective stroke, the abdomen and telson sweep anteriorly through an arc of 65-70 degrees (Figure 27c,d). Since fluid movements around the telson spines are dominated by viscous forces (Re = 0.4, see Table 8), the ventral surface of the telson pushes fluid anteriorly between the maxillipeds, toward the maxillae and mouth. At the same time, the dorsal surfaces of the abdomen and telson draw fluid in the anterior direction. At the end of the effective stroke, a redirected current moves past the mouthparts toward the antennae and rostrum (Figure 27d). Prey items are captured out of the

Figure 27. Feeding of Pugettia producta zoea larvae in moving fluid. A. Prey item approaches zoea from anterior and is propelled away by maxilliped current. Note formation of eddy downstream of the tethered zoea. Solid arrow indicates ambient current in flowtank (1.2 mm s^{-1}), open arrow shows direction of current generated by maxillipeds. Curved arrow shows trace left by dyed Patiria miniata oocyte. B. Plumose mechanoreceptor seta located on dorsal margin of the carapace. Scale bar is 25 µm. C-E. Sequence of prey capture events during sweep of the telson and abdomen. Prey items are P. miniata oocytes (130 µm dia). Solid arrcws show ambient flowtank current (1.2 mm s^{-1}), open arrows show maxilliped current. Curved arrow shows telson effective stroke. C. Time=0 s. D. Time 0.3 s. E. Time 0.9 s. Note P. miniata oocyte held by maxillae and mandibles prior to ingestion (thin arrow).


A
B
C
D
E

current by the endopodites of the 1st maxillipeds (Figure 27e). Small prey items (125-150 µm dia.) are manipulated and held by the maxillae while larger prey (>500 µm) are held by the maxillae, maxilliped endopodites and telson (Herrnkind, 1968; and personal observations).

During the recovery stroke of the abdomen and telson, the abdomen is tucked beneath the carapace and the telson is drawn posteriorly past the maxillae and maxillipeds. Abdominal muscles appear to contract sequentially beginning with the proximal segment during the recovery stroke to allow the abdominal segments to articulate while they return to their original position. The telson spines are extended distally during effective strokes (Figure 27c,d) and pointed anteriorly during recovery strokes. The 1st and 2nd maxillipeds continue to oscillate during capture and ingestion of small prey items.

The mechanism by which _Pugettia producta_ zoeae detect prey items passing over the dorsal surface of the carapace remains problematical. Visual cues do not appear to be essential in locating potential prey items since laboratory experiments conducted with _P. producta_ and other brachyuran zoeae indicate that they are capable of capturing motile and non-motile prey in complete darkness (Rumrill, 1987; Rumrill _et al_., 1985). It is possible that zoeae use tactile cues as an alternative to visual cues to detect the presence of prey items. For example, several plumose setae occur along the dorsal and lateral margins of the carapace

(Figure 27b). Each seta extends distally from a junction with the carapace and supports 40-120 setules along its length. These plumose setae are similar in appearance to tactile sensillae found in a variety of crustaceans (see Strickler and Bal, 1973; McIver, 1975). The arrangement and location of the plumose carapace setae suggest that they may function as tactile mechanoreceptors to detect local disruptions of flow along the dorsal and lateral regions of the zoea carapace. Additional putative mechanoreceptor sensillae are located along the dorsal surface of the abdomen and between the spines of the telson. The definitive function of these putative mechanoreceptors remains to be demonstrated by cinematographic, neurophysiological and histological examinations.

D. DISCUSSION

Zoea larvae of brachyuran crabs are an abundant and ubiquitous component of marine zooplankton communities (Lough, 1976; Pennington, 1986). Although several studies have investigated the diets of brachyuran zoeae (Sulkin, 1975, 1978; Sulkin and Epifanio, 1975; Sulkin and Norman, 1976; Christiansen and Yang, 1976; Levine and Sulkin, 1979, 1984; Incze and Paul, 1983; and numerous others), comparatively little attention has been given to their methods of locomotion and prey capture (Herrnkind, 1968; Gonor and Gonor, 1973; Schembri, 1982). Forward (1976, 1977) and Sulkin (1978, 1984) pointed out that locomotion and feeding are of paramount ecological significance in determining patterns of depth regulation and onshore transport in carnivorous brachyuran zoeae. However, there are several fundamental gaps in our knowledge concerning the hydromechanics of locomotion and prey capture in aquatic microcrustaceans (Lochhead, 1977). In particular, the methods employed by brachyuran zoeae to periodically accelerate and to capture and manipulate prey items are outstanding in their absence of detailed studies.

1. Locomotion of *Pugettia* Zoeae

Pugettia producta stage I and II zoeae swam in a characteristically jerky manner in the laboratory aquaria. Brief episodes of steady swimming were interrupted by frequent periods of acceleration and deceleration. In general, the swimming of a *Pugettia producta* zoea can be described as follows: 1) the zoea propels itself in the dorsal direction at an initial velocity, 2) the zoea accelerates and undergoes an increase in velocity, and 3) the zoea either accelerates again or decelerates and resumes swimming at the initial or slower speed.

The limit of temporal resolution available from the recording system used in this study was 67 ms. Consequently, results gathered by these techniques cannot be extended directly to events that occur over shorter periods of time. Strickler (1975) and Kerfoot (1978) recorded changes in swimming velocities of cyclopoid copepods and cladocerans over periods of 5 ms, and Lehman

(1977) found that a resolution of 10 ms was required to accurately determine the instantaneous velocities of a freshwater cladoceran, *Daphnia pulex*, and a calanoid copepod, *Diaptomus franciscanus*. However, the slow relative swimming velocity and large body size of *Pugettia producta* zoeae resulted in the superposition of images when they were illuminated stroboscopically at 900 pulses/min. These results indicate that valuable information about changes in the swimming velocity of a *P. producta* zoea can be obtained from consecutive measurements of displacement distances photographed with a temporal resolution of 67 ms.

Sulkin (1973, 1975, 1984) described the general pattern of swimming behavior exhibited by brachyuran zoeae. Zoeae propel themselves in the direction of the dorsal spine, and propulsive forces are generated primarily by oscillations of the 1st and 2nd maxillipeds. Similar locomotory behavior has been reported for several brachyuran zoeae (Foxon, 1934; Herrnkind, 1968; Bigford, 1979) as well as for anomuran and brachyuran zoeae with markedly dissimilar morphological traits including elongation and reduction of the dorsal and rostral spines and differences in the shape of the telson (Gonor and Gonor, 1973; Schembri, 1982). In all zoeae, propulsive forces are generated primarily by rhythmic beating of the natatory setae located on the 1st and 2nd maxillipeds. In addition, locomotion in the posterior direction can occur following rapid movement of the abdomen and telson (Gonor and Gonor, 1973; Forward, 1977). However, few details have been provided about changes in swimming velocity or rates of acceleration. In addition, there have been no previous reports concerning the movements of fluid around the zoea during locomotory behavior.

In the present study, photographs of dye-marked water indicate that the zoea carapace accelerates dorsally in response to forces generated by the displacement of fluid by the maxilliped natatory setal field. Effective strokes of the maxillipeds generate toroidal vortices that are shed by the tips of the natatory setae. Drag forces appear to arise mainly from viscous shear stresses exerted by fluid along the lateral margins of the carapace, although induced drag due to the shedding of vortices may also resist the motion of zoeae. The abdomen and telson are curved beneath the carapace and do not contribute to the generation of propulsive forces during normal swimming. Weldon (1889) suggested that the telson may aid in steering, and the orientation of the elongated telson spines in *P. producta* may also function to stabilize the zoea and reduce drag by softening the trailing edge of the rigid carapace during periods of acceleration. Lebour (1928) and Schembri (1982) noted the prevalence of rudimentary telson spines among demersal zoeae, and their observations suggest that rudimentary development of telson spines may be correlated with slow swimming velocities.

Acceleration profiles for *Pugettia producta* zoeae

indicate that changes in swimming velocity occurred at a frequency (3-5 Hz, see Figures 20-22) that was substantially slower than the rapid oscillations of the 1st and 2nd maxillipeds (21-34 Hz). Dissociation of these events suggests that each burst of acceleration is composed of between 4 and 10 oscillations of the maxillipeds.

A plausible explanation for the sinusoidal acceleration of *Pugettia producta* zoeae is that effective strokes of the 1st and 2nd maxillipeds periodically coincide to generate recurring periods of increased propulsive thrust. Several flash photographs were taken of tethered *P. producta* zoeae that caught the maxillipeds at a point of alignment along the arc of the effective and recovery stroke cycle (Figure 26). In 5 out of 7 cases, the natatory setae exhibited low deformation angles, indicating that both maxillipeds were near the completion of effective strokes. Asymmetric oscillation cycles would allow the reciprocating appendages to beat in unison for several cycles, and interaction between the 1st and 2nd maxillipeds may result in an increase in the effective surface area of the natatory setal field. Cinefilm analyses with film speeds of 200-500 frames s^{-1} are required to determine with precision the phase relationships of the maxillipeds over several hundred effective and recovery stroke cycles.

Comparisons of average relative velocity and drag forces experienced during locomotion indicate that the performance of *Pugettia producta* stage I and II zoeae follows the scaling pattern reported for various sizes of aquatic dytiscid beetles (Nachtigall, 1977; Daniel, 1984). The greatest relative velocities reached by stage II zoeae (13 body lengths s^{-1}) are comparable to those of *Dytiscus marginalis*, although they are substantially lower than the relative velocities attained by smaller water beetles (Nachtigall, 1977). The drag force, D, encountered by a *P. producta* zoea swimming at an average velocity, U, is found by

$$D = 1/2\ p\ U^2\ A\ C_d \qquad (1)$$

where p = the density of seawater, A = an estimate of the projected surface area of the zoea, and the coefficient of drag for the zoea carapace, C_d, is approximated by drag on a sphere at a Reynolds number of 5 (see Table 8). Drag forces for stage I zoeae ranged from 9.03×10^{-9} to 3.80×10^{-8} N. By comparison, the drag forces encountered by stage II zoeae were substantially higher (1.51×10^{-8} to 6.66×10^{-7} N) as a result of their faster swimming velocities and greater projected surface areas. The scaling of drag to carapace volume (exponent = 2.15) and projected surface area (exponent = 3.22) suggests that stage II zoeae must expend relatively greater effort than stage I zoeae to overcome drag. Since the majority of *P. producta* zoeae either increased or decreased their relative swimming velocities over the observation periods, drag forces associated with acceleration are an important component of zoea locomotory behavior and will be treated separately (see below).

2. Prey Capture by *Pugettia* zoeae

Although several studies indicate that phytoplankton may be a common component of the diets of brachyuran zoeae (Lebour, 1927; Atkins, 1955; Hartman and Letterman, 1978; Incze and Paul, 1983), the majority of species are omnivorous or carnivorous (Herrnkind, 1968; Mootz and Epifanio, 1974; Sulkin, 1975, 1978; Bigford, 1978). Raptorial feeding is likely the primary mode of prey capture among brachyuran zoeae, and laboratory studies demonstrate that zoeae can capture mobile invertebrate prey including rotifers, polychaete trochophores, echinoid larvae, and crustacean nauplii (Herrnkind, 1968; Sulkin, 1975; Sulkin and Epifanio, 1975; Paul *et al*., 1979; Incze and Paul, 1983; Rumrill and Chia, 1985; Rumrill *et al*., 1985; ~~and~~ several studies cited therein).

Although the principal items identified from the gut contents of brachyuran zoeae collected in the field include diatoms and dinoflagellates (Bright, 1967; Incze and Paul, 1983), phytoplankton are probably conspicuous because their thecae may be difficult to digest and have long residence times. By comparison, the remains of soft-bodied prey such as ciliated invertebrate larvae or nauplii may be difficult to detect because they have few recognizable hard parts or because the hard parts may be discarded prior to ingestion.

Observations of feeding brachyuran zoeae indicate that zoeae capture and hold their prey with their mouthparts and telson (Herrnkind, 1968; Schembri, 1982) and shred portions of the prey with the mandibles. However, recognizable fragments of echinoid pluteus larvae were found in the gut contents of stage I zoeae of the grapsid crab, _Hemigrapsus nudus_ at the termination of laboratory feeding experiments (Rumrill and Chia, 1985).

The feeding behavior of _Pugettia producta_ zoea larvae observed in the present study is consistent with Herrnkind's (1968) observation of "tail lashing" during the capture of _Artemia_ nauplii by zoea larvae of _Uca pugilator_. However, the mechanism for capturing small prey items would not have been predicted from Herrnkind's (1968) description of the use of the telson spines to pin prey against the rostrum prior to ingestion. In _P. producta_, small prey items, including asteroid oocytes and embryos, were captured out of an anteriorly directed feeding current by movements of the endopodites of the 1st maxillipeds and maxillae. There was no evidence of direct contact between the telson and prey items during bouts of feeding upon _Patiria miniata_ oocytes and embryos. However, contact with the telson did occur during the capture of larger prey such as _P. miniata_ bipinnaria larvae. Asteroid bipinnaria and echinoid pluteus larvae were pinned by the telson prior to ingestion in a manner similar to that reported by Herrnkind (1968; Rumrill, pers. observations). Although the concentration of prey items was abnormally high in the observation chamber, the ingestion rates by _P. producta_ were well below saturation levels (see Rumrill, 1987).

3. Comparison between Brachyuran Zoeae and Other Aquatic Arthropods

In contrast to the wealth of information gathered concerning the swimming behavior and feeding mechanisms of copepods (Kabata and Hewitt, 1971; Strickler, 1975, 1977, 1982; Koehl and Strickler, 1981; Alcaraz _et al_., 1980; Andrews, 1983), cladocerans (Lehman, 1977; Lochhead, 1977; Kerfoot, 1978) and dytiscid beetles (Nachtigall, 1977; Nachtigall and Bilo, 1975), the mechanisms by which brachyuran zoea swim and capture prey are poorly understood. Comparisons of swimming and feeding between _Pugettia producta_ zoeae and other aquatic arthropods reveal several fundamental similarities in the hydromechanics of locomotion and removal of particles from fluid at low Reynolds Numbers.

Like that of brachyuran zoeae, the swimming behavior of copepods and cladocerans can be characterized by rapid changes in direction and velocity (Strickler 1975; Lehman, 1977). Propulsive forces and changes in swimming velocity are generated primarily by movements of the antennae, mandibular palps, maxillae and thoracic legs in calanoid copepods (Gauld, 1966; Anderson, 1974; Strickler, 1975, 1977), and by oscillations of the 1st antennae, thoracic legs and abdomen in cyclopoid copepods (Strickler and [illegible]

1973). Propulsive forces are generated in cladocerans by rhythmic beating of the biramous 2nd antennae (Lochhead, 1977). In all of these microcrustaneans, the reciprocating appendages generate force vectors that propel the organism through water at cruising speeds on the order of 5 to 50 mm s^{-1}. However, instantaneous swimming velocities can reach 500 mm s^{-1} in copepods, and their rates of acceleration have been reported to be as high as 12000 mm s^{-2} (Strickler, 1975). Similarly, the velocities reached by cladocerans during escape responses are typically between 60 and 90 mm s^{-1} with acceleration rates of up to 3250 mm s^{-2} (Lehman, 1977). Although Reynolds numbers at these maximum swimming velocities approach 500, information from velocity profiles indicates that streamlines around the exoskeleton are laminar rather than turbulent (Lehman, 1977; Kerfoot *et al.*, 1980).

In contrast to copepods and cladocerans, propulsive forces are generated in brachyuran zoeae by oscillations of the 1st and 2nd maxillipeds. During effective strokes, lateral sweeping movements of the maxillipeds cause fluid to shear past the margins of the carapace. Beating of the telson does not appear to be essential in the generation of propulsive forces in *Pugettia producta* zoeae. The maximum swimming velocity recorded for *P. producta* in the present study was 13 mm s^{-1}, although velocities as high as 22 mm s^{-1} have been reported during positive phototaxis of [illegible] idus stage VII zoeae (Sul

Since the swimming velocities and maximum acceleration rates of copepods and cladocerans with comparable body sizes are typically greater than those of brachyuran zoeae, the drag forces exerted by fluid against the copepod and cladoceran exoskeletons are also expected to be substantially higher. Strickler (1975) and Kerfoot _et al_. (1980) suggested that the teardrop and torpedo shapes of cyclopoid and calanoid copepods may reflect the importance of streamlining to reduce drag. Conversely, the relatively globose body plans of brachyuran zoeae and small dytiscid beetles (Nachtigall, 1977) are common among aquatic arthropods where drag forces take on less importance than frictional forces.

Visualization of fluid dynamics revealed that the viscous effects of seawater govern mechanisms of prey capture in calanoid copepods (Alcaraz _et al_., 1980; Andrews, 1983). Koehl and Strickler (1981) described the movements of feeding currents generated by beating of the 2nd antennae, mandibular palps, 1st maxillae and maxillipeds in _Eucalanus pileatus_. Movements of the 2nd maxillae were observed to draw fluid containing food particles toward the mouth where algal cells are captured and ingested (Alcaraz _et al_., 1980; Paffenhofer _et al_., 1982). These cinematographic studies demonstrate that algal cells are captured along with parcels of fluid by rapid movements of the 2nd maxillae. Similarly, observations of the movements of dye-marked water and episodes of feeding upon asteroid oocytes made during this study indicate that the viscosity of sea water also plays an important role in the mechanism of prey capture in Pugettia producta. The 2nd maxillae of E. pileatus and endopodites of the 1st maxillipeds of Pugettia producta are both surrounded by relatively thick boundary layers, and each appendage operates at a Reynolds number of about 10^{-2} (see Table 8). Consequently, these appendages can be expected to function similarly in their capacity to draw prey items toward the mouth along with associated parcels of viscous fluid.

Despite hydromechanical similarities in the low Reynolds number flows associated with the feeding appendages of copepods and brachyuran zoeae, several pronounced differences are apparent when comparisons are made between the feeding mechanisms of carnivorous copepods and that of Pugettia producta stage I and II zoeae. First, carnivorous cyclopoid and calanoid copepods use the 2nd maxillae to capture and hold their prey (Ambler and Frost, 1974; Landry, 1978; Lonsdale et al., 1979; Koehl and Strickler, 1981). In Cyclops scutifer, swimming prey are attacked while they are 0.5 to 2 body lengths away from the copepod, and most prey are captured within a cone-shaped region that extends anteriorly between the antennae (Kerfoot, 1978). In contrast, the majority of prey attacked by crustacean zoeae are captured after they enter a spherical region located ventrally between the endopodites of the 1st maxillipeds (Moller, 1978; Rumrill *et al*., 1985). Second, although *C. scutifer* and *P. producta* zoeae are both encounter predators that rely on tactile cues to detect the presence of prey, the copepods scan the water to detect disturbances with mechanoreceptors located on their 1st and 2nd antennae (Strickler, 1975; Poulet and Marsot, 1978; Andrews, 1983). In contrast, *P. producta* zoeae appear to detect prey via mechanoreceptors located on dorsal surface of carapace. Finally, unlike carnivorous copepods, *P. producta* zoeae use the telson to redirect fluid containing small prey items toward the mouth. Furthermore, the telson can also be used to capture and hold relatively large and active prey items.

During the capture of small prey items, the endopodites of the 1st maxillipeds and maxillules of *P. producta* zoeae select individual prey items from a passing parcel of water and manipulate them into the mouth. In contrast, herbivorous copepods, such as *Eucalanus pileatus*, sieve water between setae located on the 2nd maxillae, thereby retaining algal cells by a combination of active capture and filtration.

4. *Importance of the Acceleration Reaction*

Predatory microcrustaceans can play a major role in the regulation of species composition and demographic structure of freshwater and marine zooplankton communities (Dodson, 1974; Kerfoot, 1977, Kerfoot *et al*., 1980; Landry, 1978; Zaret, 1980). Recent attempts to model quantitatively the effects of selective predation in zooplankton communities are based on the simplifying assumption that predator and prey swimming speeds are constant and unidirectional in time and space (Gerritsen and Strickler, 1977; Greene, 1983). However, Daniel (1984) argues that steady-state motion is rare in aquatic locomotion; swimming organisms typically accelerate to attack prey and to escape predation. Furthermore, unsteady flow is frequently generated by oscillating paired swimming appendages during episodes of propulsive thrust and turning (Daniel, 1983). Since periodic changes in velocity are an integral component of locomotion in aquatic microcrustaceans, it is a central problem to gauge the relative importance of unsteady aspects of swimming, particularly as they apply to short-term events associated with locomotory behavior and prey capture.

The reciprocating maxillipeds of a _Pugettia_ _producta_ zoea generate instantaneous force vectors at the end of their effective strokes that propel the larva through water in a jerky manner (see Figures 18-22). Daniel (1984) pointed out the mechanism by which the acceleration reaction, or the forces that resist changes in static velocity, can be utilized by aquatic arthropods such as dytiscid beetles to generate thrust during locomotory behavior characterized by unsteady motion. In _P_. _producta_, the instantaneous acceleration reaction (G) can be approximated by

$$G = -L\ p\ V\ (du/dt) \qquad (2)$$

where L is the added mass coefficient for a sphere (0.5), p is the density of seawater, V is an estimate of the displacement of the zoea carapace, and du/dt is an estimate of instantaneous acceleration. The acceleration reaction can be found by integrating G over any specified time interval T, such that

$$1/T \int -L\ p\ V\ (du/dt)\ dt \qquad (3)$$

Two time intervals, T_s and T_f, are particularly relevant. The first time interval, T_s, is defined as the period of time required for a *Pugettia producta* zoea to accelerate from cruising to maximum swimming speed. The second time interval, T_f, is the time required for a zoea to detect and capture a prey item. In *P. producta*, acceleration to the maximum observed swimming speed takes from 201 to 268 ms, and the time required to capture and secure a prey item is about 300 ms. The acceleration reaction has a value of -5.99×10^{-10} N for a stage I zoea that accelerated from 2.6 to 3.7 mm s^{-1} over a period of 201 ms. Similarly, an acceleration reaction value of 8.68×10^{-9} N occurs for a stage II zoea that accelerated from 5.7 to 11.1 mm s^{-1} over a period of 268 ms. These force values are estimates of the negative resistance that must be overcome in addition to drag for the zoeae to accelerate.

The relative importance of the acceleration reaction (I) can be represented by a dimensionless ratio of the forces resisting acceleration over the total (acceleration and drag) resistive force as

$$I = G / G + D \tag{4}$$

The ratio I has a value of 1.66×10^{-2} or approximately 1.7% for the stage I zoea over the time interval T_s. The acceleration reaction contributes 1.93×10^{-2} (1.9%) of the total resistive force in the stage II zoea. Since the ratio I can only have values between 0 and 1.0, the low values indicate that drag forces, rather than acceleration forces, dominate the swimming motion of P. producta zoeae during T_s. The resistive forces due to acceleration decrease to about 0.5% when I is figured over the time interval required to capture prey, T_f. Since laboratory observations presented here indicate that P. producta zoeae capture non-motile and slow moving prey by redirecting fluid containing prey items past the feeding appendages and mouthparts, the resistive forces that must be overcome during an encounter with a prey item are expected to be minor compared with the forces that resist changes in velocity during acceleration or escape maneuvers by zoeae in response to other zooplankton predators.

E. CONCLUSIONS

Sulkin *et al*. (1980) and Kelly *et al*. (1982) developed models for the recruitment of brachyuran larvae that are based upon ontogenetic differences in the swimming behavior of zoea stages. Similarly, Cronin (1982) and Cronin and Forward (1982) reported that differences in larval swimming behavior result in the retention of *Rithropanopeus harisii* zoeae within regions of a shallow estuary and net transport of *Callinectes sapidus* out of the estuary. The importance of zoea locomotory behavior is conspicuous in these studies, and they indicate that changes in the rate and direction of zoea swimming can play a central role in the behavioral basis of depth regulation (Sulkin, 1984). Consequently, quantitative descriptions of swimming behavior contribute to an understanding of the larval ecology of brachyurans by providing useful information about average swimming velocities and rates of acceleration within water masses.

The observations reported here corroborate previous studies of zoea behavior (Herrnkind, 1968; Schembri, 1982), and provide a more detailed description of the locomotory mechanisms utilized by brachyuran zoeae. Fluid movements around tethered zoeae have important implications concerning the maxilliped propulsion system and mechanisms of prey capture, but information concerning flow patterns around unrestrained zoeae are required to fully appreciate the range of behavioral responses and functional anatomy of the conservative brachyuran zoea body plan. Since intraspecific variation in zoea swimming behavior was considerable in Pugettia producta, it is premature to extrapolate the results of this study to larger groups of sibling zoeae or to the behavior of zoea populations in nearshore waters. Nevertheless, generalizations concerning average swimming velocities and mechanics of prey capture reported here may be warranted for zoeae of other brachyuran crabs. Knowledge about these fundamental aspects of larval behavior can contribute to an understanding of the complex processes affecting the selection of prey items, dietary requirements and distribution of planktonic brachyuran zoeae.

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CHAPTER V.

RECRUITMENT OF ASTERINA MINIATA (BRANDT, 1835): A POST-FACTO ASSESSMENT OF LARVAL ABUNDANCE, SUBSTRATUM SELECTION, AND LARVAL PREDATION

A. INTRODUCTION

Spatial and temporal variability in the abundance and distribution of early juveniles are prominent features of benthic marine invertebrate populations (Coe, 1956; Ebert, 1983; Caffey, 1985; Connell, 1985). General concepts of invertebrate recruitment consider interactions between events that occur in the plankton, during settlement, and on the bottom to determine patterns of juvenile distribution (Cameron and Schroeter, 1980; Cameron and Rumrill, 1982; Keough and Downes, 1982; Underwood and Denley, 1984; Connell, 1985; Gotelli, 1987). Factors that contribute to larval availability include: 1) physical and biological oceanic processes that regulate the spatial patchiness of larval populations (DeWolf, 1973; Omori and Hamner, 1982; Keough, 1983; Grosberg, 1982; Cameron and Rumrill, 1982; Emlet, 1986; Jackson, 1986), 2) rates of larval differentiation and growth (Jackson and Strathmann, 1981; Roller and Stickle, 1985; Paulay et al., 1985), and 3) mortality prior to the onset of metamorphic competence (Thorson, 1966; Hancock, 1973; Rumrill and Chia, 1985; Rumrill et al., 1985; Young and Chia, in press). Near the end of the planktonic period the availability of suitable sites for settlement (Grosberg, 1981; Young and Chia, 1982; Highsmith, 1982; Cameron and Schroeter, 1980; Breitburg, 1984) and the distribution and efficiency of benthic predators (Thorson, 1950, 1966; Wilson, 1980) regulate the initial distribution of newly settled post-larvae. Finally, the intensity of recruitment is determined after settlement by: 1) the initial abundance of post-larvae, 2) early mortality rates, and 3) immigration and emigration from the settlement site following metamorphosis (Woodin, 1976, 1978; Oliver _et al_., 1982; Young and Chia, 1984; Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Watzin, 1986). Complex interactions between these pre- and post-settlement events can lead to uncertainty in understanding the causes of spatial and temporal variation in the recruitment of benthic invertebrates (see Connell, 1985 for review).

Few studies of echinoderm populations distinguish between settlement, defined as the place and time when a larva becomes temporarily attached to the substratum, and recruitment, defined as the time when the smallest individuals can be accurately censused in the field. Settlement and recruitment of long-lived, iteroparous asteroids can vary markedly in space and time (Burkenroad, 1957; Loosanoff, 1964; Yamaguchi, 1973; Ebert, 1983). Consequently, it is likely that local settlement events are frequently overlooked until juveniles grow large enough to be sampled in the field. The time between settlement and recruitment can be brief or nonexistent in asteroids that brood offspring or that have macroscopic post-larvae (Chia, 1966; Menge, 1975; Strathmann _et_ _al_., 1982). In contrast, the comparatively small size and slow growth rates of post-larvae that develop from planktotrophic brachiolariae typically result in long intervals between settlement and recruitment. Field studies provide inferential evidence that recruitment may be separated from settlement by 3 to 9 weeks among tropical asteroids (Yamaguchi, 1973) and by 5 to 13 months among temperate species (Vevers, 1949; Barnes and Powell, 1950; Quayle, 1954; Feder, 1970; Barker, 1977). A long interval between settlement and recruitment necessitates a post-facto approach to evaluate the importance of pre-settlement and post-settlement processes in determining spatial and temporal patterns of recruitment.

The asterinid sea star, _Asterina_ _miniata_ (Brandt, 1835), is a common member of shallow-water, soft-sediment, invertebrate communities along the west coast of Vancouver Island (Appendix I). In Barkley Sound, populations of _A_. _miniata_ occur in protected areas adjacent to eelgrass beds (_Zostera_ _marina_ L.). Other conspicuous members of these soft-sediment communities include the alga, _Gracilaria_ _pacifica_ (Abbott, 1980), the burrowing cerianthid anemone, _Pachycerianthus_ _fimbriatus_ McMurrich, 1910, and the phelebobranch ascidian, _Corella_ _willmeriana_ Herdman, 1898. Individuals of _A_. _miniata_ are predators of urchins and bryozoans in rocky subtidal habitats in southern California (Day and Osman, 1981; Schroeter *et al*., 1983) and they play a major role in the dynamics and utilization of drift algae in kelp forests (Gerard, 1976). In the Pacific Northwest, individuals of *A*. *miniata* are important scavengers within shallow-water soft-sediment estuarine communities (Rumrill, personal observations).

In this study, a heterogeneous spatial pattern of recruitment in *Asterina miniata* between adjacent estuarine inlets is described. A post-facto approach was used to evaluate pre-settlement and post-settlement factors that contribute to the differential pattern of recruitment. These factors include: 1) temporal and spatial heterogeneity of larval populations, 2) larval substratum selection, 3) predation upon larvae at the time of settlement, 4) mortality rates of juveniles, and 5) rates of juvenile immigration and emigration. Two assumptions are implicit: 1) larval behavior and substratum selection of *A*. *miniata* do not vary significantly between successive breeding seasons, and 2) interspecific variability in predation upon larvae exceeds temporal differences in predation between conspecific suspension feeders. The results provide empirical and conceptual evidence that larval substratum selection and predation during settlement are key determinants of spatial variability in recruitment. A second conclusion is that advantages associated with repeated sampling of substrata for a suitable settlement site are offset by increasing the cumulative risk of predation by benthic suspension feeders.

B. MATERIALS AND METHODS

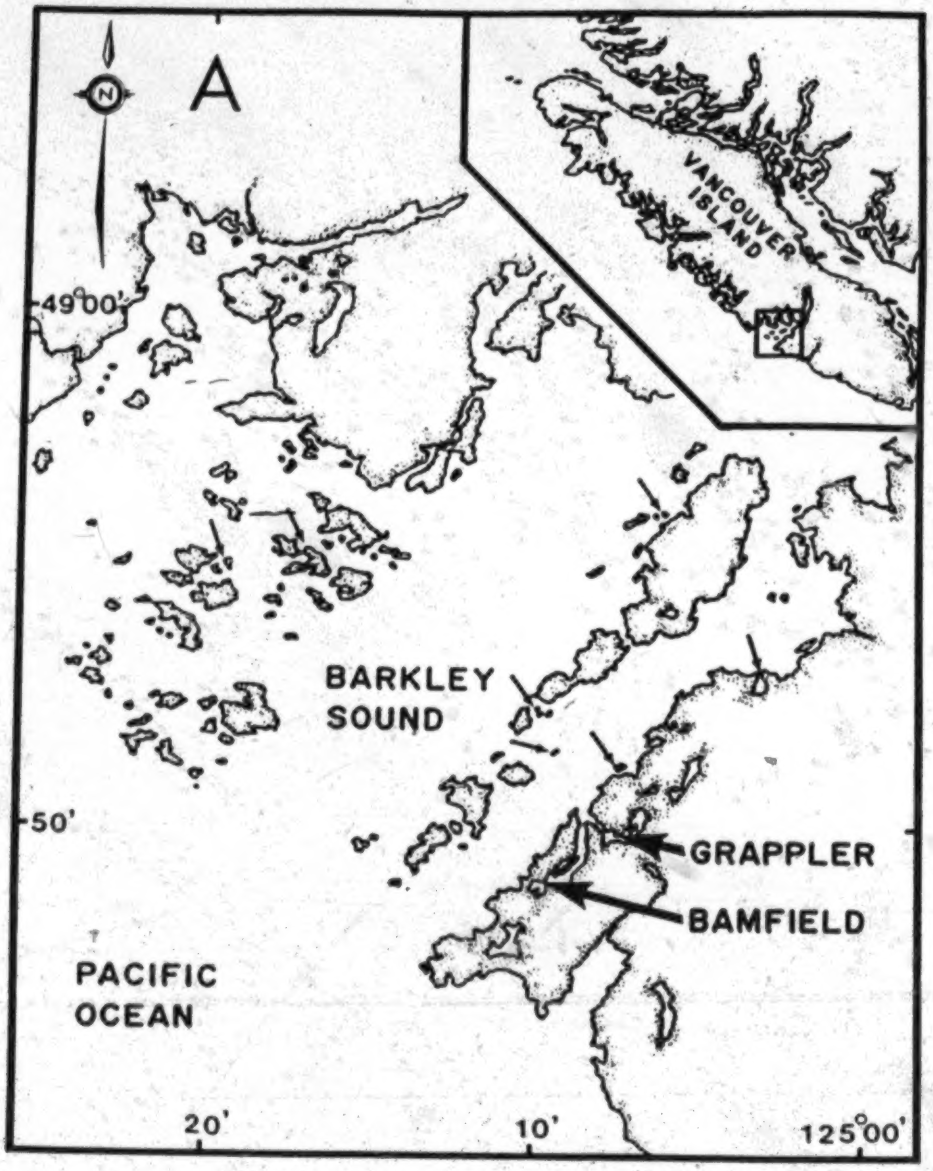
1. Study Sites

The research was carried out between March 1985 and February 1986 at 2 sites near Bamfield Marine Station, on the west coast of Vancouver Island, British Columbia (48° 50'N, 125° 08'W). Bamfield and Grappler Inlets are estuarine tidal channels that extend inland for about 2.5 km from Barkley Sound (Figure 28). Tides in the inlets are mixed and semi-diurnal with a vertical range of 3.6 m. The study sites were located at depths of 5 to 7 m on mud and cobble substrata near the heads of the inlets. Each site was inhabited by a large population of *Asterina miniata*. The nearest known other populations of *A. miniata* are located 5 and 7 km from the mouth of the inlets. Ambient surface temperature and salinity were measured at the sites at haphazard phases of the tidal cycle.

2. Abundance and Recruitment of Asterina

Size-frequency distributions of *Asterina miniata* populations were estimated during March through December 1985 at the Bamfield and Grappler Inlet study sites. Square quadrats (0.25 m^2) were placed in contiguous sets of 4 along 50 m transect lines to cover 50 m^2 at each study site. Size-frequency data for *A. miniata* were obtained by measuring the ray lengths of all individuals that occurred

Figure 28. Field sites in Barkley Sound, Vancouver Island, British Columbia. A. Barkley Sound. Labelled arrows show *Asterina miniata* study areas in Grappler and Bamfield Inlets. Unlabelled arrows indicate locations of other known populations of *A. miniata*. B. Bamfield and Grappler Inlets. G-HR indicates location of high recruitment site in Grappler Inlet; B-LR shows low recruitment site in Bamfield Inlet. P-1, P-2, and P-3 show zooplankton sample sites. AP indicates source of sediments for substratum selection experiments (see Tables 14 and 15).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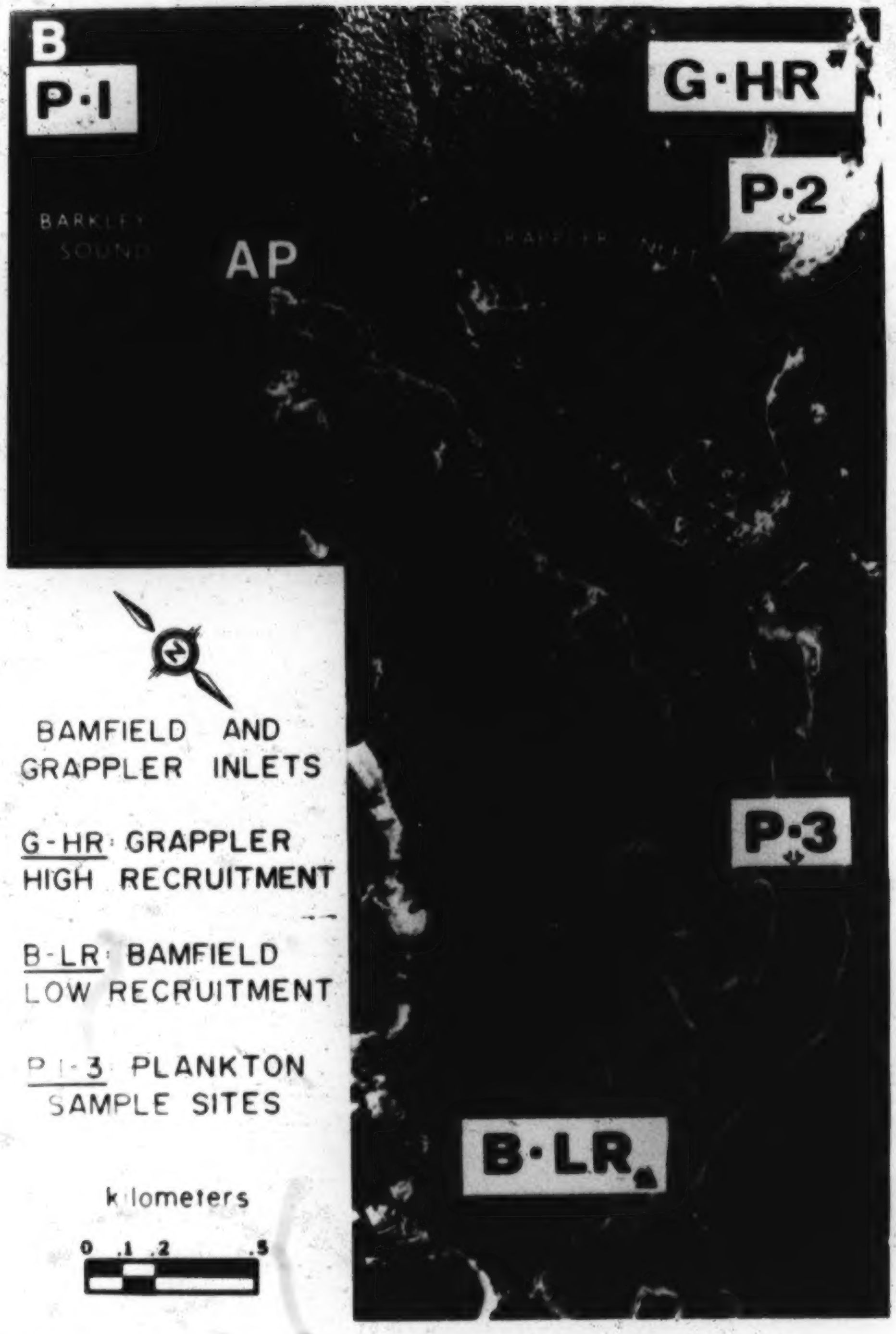
B
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G·HR
P·2
BARKLEY SOUND
AP
GRAPPLER INLET
P·3
B·LR
BAMFIELD AND GRAPPLER INLETS
G-HR: GRAPPLER HIGH RECRUITMENT
B-LR: BAMFIELD LOW RECRUITMENT
P 1-3 PLANKTON SAMPLE SITES
kilometers
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within quadrats. Subtidal counts and measurements of *A. miniata* and other benthic marine invertebrates (see Table 16) were made *in situ* using SCUBA. Additional *A. miniata* were measured at each site in May and June, 1985 during an extensive search for juveniles. Ray length measurements were recorded for all *A. miniata* that occurred along a second 50 m line adjacent to the initial transect.

3. *Reproductive Activity of Asterina*

Seasonal reproductive activity of *Asterina miniata* was followed to estimate the time of spawning and migration of embryos and early larval stages into the plankton. Allocation to somatic and reproductive tissue was assessed by methods outlined by Giese and Pearse (1974). Every other month, from March 1985 to February 1986, twenty-five adults of *A. miniata* were collected near the Grappler Inlet site. Gonads and pyloric caecum tissues were separated into pre-weighed dishes and dried at 22-24°C to constant weight. Remaining parts of the body were pooled into a third dish and dried and weighed. Gonad index and pyloric caecum index values were computed as:

(excised tissue wt./total body wt.) X 100.

4. *Larval Distribution and Abundance*

The abundance and distribution of asteroid larvae was estimated from a time-series of zooplankton tows. Since it was not possible to distinguish bipinnariae and brachiolariae of *Asterina miniata* from those of other species, total numbers of asteroid larvae were counted to obtain estimates of abundance and spatial distribution. It was assumed that the distribution and behavior of *A. miniata* larvae were similar to that of other species collected by plankton nets. There are no empirical data to either support or refute such an assumption. Asteroid bipinnaria and brachiolaria larvae were collected at 3 sites from zooplankton tows taken with 125 µm mesh, 0.5 m diameter standard and closing nets. During each sampling period, three replicate oblique samples were taken from the water column near the Bamfield Inlet and Grappler Inlet sites. Plankton samples were collected with a closing net at 30, 60, and 90 m depths at a site near the mouth of the inlets (Figure 28b, site P-1). Tows were taken at approximately 3 wk intervals from March, 1985 to February, 1986. No samples were taken in January, 1986. Each tow was preserved in 10% buffered formalin immediately after collection and sorted under a stereomicroscope.

5. Larval Substratum Selection

Gametes obtained from gravid *Asterina miniata* following injections of 10^{-5} M 1-Methyladenine or from natural spawnings were reared in the laboratory in 3.78 liter glass jars at ambient sea temperatures (11-15°C). Bipinnaria and brachiolaria larvae were cultured at densities of 100-150 larvae liter^{-1} in aerated jars equipped with slowly oscillating paddles. Larvae were fed a mixture of *Dunaliella tertiolecta* Butch. and *Pavlova lutheri* Droop every 3 to 4 days at the time sea water in the culture vessels was replenished. Cultures initiated at various times throughout the study provided developmental stages for predation experiments with Pachycerianthus fimbriatus and Corella willmeriana.

A series of 4 laboratory experiments examined substratum selection at settlement by brachiolaria larvae of Asterina miniata. Settlement experiments of a multiple substratum design were conducted in glass petri dishes (10 cm diameter) coated by thin layers of 5% agar in seawater. Substrata from Grappler Inlet included sediments, bivalve shell fragments (Tresus nuttali), rocks and 3 species of algae (Ulva sp., unidentified crustose coralline algae, and Gracilaria pacifica). Clean and aged glass were also included. Aged substrata were prepared by placing shell fragments, rocks and glass into running unfiltered seawater for 2 wks prior to the experiment; during the 2 wk period a surface film composed of bacteria, diatoms and other microorganisms developed. Substrata were arranged in the petri dishes at random according to a Latin square, and each presented a surface area of approximately 1 cm^2. Three trials were conducted with 8 substrata and 20 brachiolaria larvae per dish.

Single substratum experiments compared rates of settlement and metamorphosis on sediments collected from Bamfield and Grappler Inlets. Sediments from a third site near the entrance of Bamfield Inlet were also tested (Figure 28b, site AP). A 5 mm layer of sediment was placed at the bottom of 250 ml beakers, and each was filled with 180 ml of 1 µm filtered seawater. At the initiation of the experiment either 50 or 20 Asterina miniata brachiolariae were pipetted gently into the center of each beaker. Experiments were carried out under 16L:8D photoperiod and consisted of 4 replicates with sediment and 4 controls without sediment.

Single substratum experiments (4 replicates of each treatment, 15 larvae per trial) were also conducted to compare rates of settlement and metamorphosis between fresh and aged sediments from the entrance of Bamfield Inlet (Figure 28b, site AP). Sediments were aged in running unfiltered seawater for 9 days prior to each trial. Substrata were examined for recently metamorphosed Asterina miniata at intervals of 24 hours over a period of 3 days in all substratum selection experiments.

6. Predation upon Larvae by Benthic Suspension Feeders

Predation upon settling larvae by benthic suspension feeders was assessed by: a) the examination of gut contents, b) laboratory feeding experiments, and c) estimation of predator-prey encounter rates.

a. Analysis of Gut Contents

Gut contents of Pachycerianthus fimbriatus and Corella willmeriana were examined to determine whether the size range of prey items corresponded to that of settling larvae of Asterina miniata. Individuals of P. fimbriatus (n = 17) and C. willmeriana (n = 27) collected from Grappler and

Bamfield Inlets on August 5-6, 1985 were immediately preserved in 30% buffered formalin. Gut contents from each specimen were stained with phloxine B (Mason and Yevich, 1967) and examined at a magnification of 12X under a stereomicroscope. Although counts were made of the various taxonomic groups of prey items, only data concerning prey sizes are presented here.

b. Laboratory Predation Experiments

Laboratory feeding experiments examined the stage-specific and density-dependent (functional response, sensu Holling, 1966) characteristics of predation by *Pachycerianthus fimbriatus* and *Corella willmeriana* upon *Asterina miniata* embryos and larvae. Stage-specific feeding experiments were carried out with six developmental stages of *A. miniata* including: 1) zygotes, 2) embryos, 3) blastulae, 4) late gastrulae, 5) bipinnariae, and 6) brachiolariae (Table 9). Functional response experiments were conducted at 6 prey densities with two developmental stages (embryos and bipinnaria larvae).

Stage-specific feeding experiments were carried out with *Pachycerianthus fimbriatus* following methods developed for a terebellid polychaete (Wilson, 1980). A series of 2 liter circular aquaria were used each containing a loop of 12.7 mm diameter latex tubing. Individuals of *P. fimbriatus* constructed mucus-lined burrows in the tubes and extended their tentacles in a manner similar to that observed in the field. A few individuals were maintained in artificial

TABLE 9

Developmental stages of *Asterina miniata* used in feeding experiments with *Pachycerianthus fimbriatus* and *Corella willmeriana*. Table entries show sample size, mean and s.d. of size measurements. Measured dimensions: a, diameter; b, greatest length; c, greatest length & greatest width.

DEVELOPMENTAL STAGE	CODE	APPROXIMATE SHAPE	DIMENSION (n)	MEAN (µm)	S.D. (µm)	SWIMMING BEHAVIOR
Zygotes	ZYG	Spherical	a (34)	137	(6)	non-motile
Embryos	EMB	Spherical	a (23)	267	(26)	non-motile
Blastulae	BLS	Spheroid	b (28)	429	(28)	forward
Gastrulae II	GST	Prolate Spheroid	b (33)	526	(43)	forward
Bipinnariae	BIP	Ellipsoid	c (21)	L: 1028 W: 597	(66) (37)	forward & reverse
Brachiolariae	BCH	Elongate Ellipsoid	c (16)	L: 1194 W: 561	(72) (33)	forward & reverse & loop

tubes for over 4 months. Aquaria previously inhabited by anemones served as control chambers to assess handling losses and the effects of tubes. The experiments consisted of 5 - 10 replicate treatments with anemones and 3 - 6 controls without anemones (see Figure 37). Initial prey densities were 100 embryos of larvae liter^{-1}. Seawater in the aquaria was continuously agitated by a slow stream of small air-bubbles. The number of Asterina miniata survivors was determined after a period of 12 hrs following concentration into a small volume of seawater. Surviving embryos and larvae were fixed in buffered formalin and counted in a Bogorov tray.

Stage-specific feeding experiments with Corella willmeriana followed a modification of the design of Rumrill et al. (1985). Basal regions of the ascidians were attached to the insides of plastic jar lids with Krazy glue cyanoacrylate adhesive. The lids were sealed over 250 ml glass jars containing embryos or larvae of Asterina miniata at an initial density of 100 prey liter^{-1}. Stage-specific feeding experiments with C. willmeriana consisted of 7 replicates with ascidians and 3 controls without ascidians. Jars were fastened to a motor-driven cage and rotated continuously at 4 rpm. The number of surviving A. miniata embryos and larvae was determined after 1 hr.

Feeding experiments were carried out in a seawater flume (L:58 X W:8 X H:7 cm) to examine the responses of Pachycerianthus fimbriatus and Corella willmeriana to increasing prey density under conditions of unidirectional flow. Seawater was circulated by an airlift at a velocity of 0.3 cm s^{-1}. Individuals of P. fimbriatus and C. willmeriana were allowed to equilibrate for 4 hrs in the working section of the flume. Embryos or larvae of Asterina miniata were placed into a holding chamber positioned upstream from the working section. At the beginning of each trial, embryos or larvae were allowed to flow past the predator. The capture of prey and larval behavior were observed through a stereomicroscope mounted above the working section of the flume. Density-dependent feeding experiments were conducted at initial densities of 10, 25, 50, 100, 200, and 500 prey per liter, and each consisted of 3 replicates with predators and 3 controls without predators. The number of embryos or bipinnaria larvae captured was determined by subtracting the number of survivors recovered at the end of the experiment from the initial number of prey. All experiments were about 30 min in duration and were conducted under constant illumination from fluorescent lamps in a cold room at 13°C.

c. Predator Encounter Rates

Ambient current velocities were measured in situ by divers at the Bamfield and Grappler Inlet study sites on 3 occasions (June 6, 16, and August 8, 1985) during periods of peak flood and ebb tidal flow. During each series of measurements, divers released fluorescein dye from a syringe at a point 10 cm above the bottom. Advection of the dye over a distance of 50 cm was timed with a stopwatch. Current velocities were measured 5 to 9 times during each sampling period.

Size distribution, height above the substratum, and feeding posture of Pachycerianthus fimbriatus tentacles were determined for 41 animals in situ at the Grappler Inlet study area from a series of underwater photographs. All photographs included a cm scale ruler to correct for magnification errors. Densities of Corella willmeriana were estimated in Grappler and Bamfield Inlets on 5 occasions between May and December 1985 from 10 sets of 4 contiguous 0.25 m^2 quadrats placed at random points along a 30 m transect line. All ascidians within the quadrats were placed into plastic bags by divers and returned to the laboratory for counting and measurements. The body length, siphon radius, and instantaneous volume of water affected by the feeding activities of C. willmeriana were measured for 29 individuals. Measurments of siphon radii were made with an ocular micrometer while the ascidian was actively pumping seawater in the flume. Estimates of the velocity of the feeding current, and height and radius of the feeding current paraboloid (see Figure 42c) were determined by tracing the streamlines of Nile Blue dyed seawater.

The filtration efficiencies of Pachycerianthus fimbriatus and Corella willmeriana were estimated from direct observations of predation during density-dependent feeding experiments. A total of 233 embryos and 126 bipinnaria larvae of Asterina miniata were observed as they encountered the marginal tentacles of P. fimbriatus or the feeding current paraboloid of C. willmeriana. The fate of the A. miniata embryo or larva (captured or escaped) was recorded after the encounter with P. fimbriatus or C. willmeriana.

7. Juvenile Survivorship

Seven laboratory experiments during April and May 1985 assessed the susceptibility of juvenile Asterina miniata to predation by benthic macroinvertebrates and fish. Juveniles of A. miniata collected from Grappler Inlet had ray lengths between 0.8 and 2.7 cm. Predatory macroinvertebrates and fish collected near the study site included asteroids (Pisaster brevispinus, Evasterias troschelli, Dermasterias imbricata, A. miniata), cancrid crabs (Cancer productus, C. magister) and juvenile ling cod (Ophiodon elongatus). In each trial, a single predator and 5 juvenile P. miniata were placed into a plastic tub (L:55 X W:40 X H:30 cm) containing a layer of sediment from Grappler Inlet. Predation experiments with P. brevispinus and O. elongata were conducted in larger tubs (L:100 X W:70 X H:30 cm). All tubs were covered with nylon mesh and supplied with running seawater. The number of surviving A. miniata was monitored over a period of 2 to 4 weeks.

Field predation experiments were carried out with Cancer productus. Five juvenile A. miniata were placed into each of 4 cages (L:50 X W:50 X H:25 cm) covered with 0.5 cm plastic mesh. The cages were anchored along a transect line in Grappler Inlet. At the initiation of the experiment an adult male C. productus was placed into each of 3 cages. The fourth cage did not contain a crab and served as a control to assess losses due to escape from the cages. All 4 cages were retrieved after 6 days and the number of remaining A. miniata was counted.

8. Juvenile Immigration and Emigration

Rates of movement by Asterina miniata post-larvae and juveniles were measured in order to infer whether immigration or emigration could be a factor in the establishment of heterogeneous size-frequency distributions between Bamfield and Grappler Inlets. Crawling speed was measured for 37 individuals of A. miniata as they moved across detritus and mud on the bottom of glass petri dishes or a sea table. The ray lengths of A. miniata ranged from 0.6 to 2.6 cm. A. miniata that crawled continuously for less than 12 seconds were excluded from consideration

Statistical analyses were carried out following methods outlined by Snedecor and Cochran (1967), Daniel (1978), and Sokal and Rohlf (1981).

C. RESULTS

1. Study Sites

Populations of Asterina miniata occur in similar habitats at the Bamfield and Grappler Inlet study sites (Figure 28). Both populations are located near eelgrass beds and mudflats at depths of 5 to 7 m. Sea surface temperatures varied seasonally from 5.6 to 17.1 C in Bamfield Inlet and from 4.8 to 17.9 C in Grappler Inlet (Figure 29). Surface temperatures in Trevor Channel were generally 0.5°C cooler than in the inlets. Surface salinities varied seasonally between 24-25 0/00 in the spring and 27-28 0/00 during late summer and fall months. Both populations of A. miniata were exposed to similar current velocities (7-24 cm s^{-1}) during tidal exchange.

2. Abundance and Recruitment of Asterina

Densities of Asterina miniata averaged 2.69 ± 0.59 m^{-2} at Bamfield and 3.46 ± 0.65 m^{-2} at Grappler Inlet. Size-frequency analysis showed a marked difference in the size structure of A. miniata populations between Grappler and Bamfield Inlets (Figure 30). Both populations were composed largely of adults at reproductive size with ray-lengths between 7 and 11 cm. Two distinct cohorts of small individuals occurred in Grappler Inlet. In March 1985, age-1 juveniles made up 10.2% of the sample with a mean ray length of 0.9 cm. The intermediate age-2 cohort made up 6.6% of the sample with a mean ray length of 3.1 cm. The age-1 and 2 cohorts increased steadily in size and remained nearly constant in abundance over the 12 month period of study (Table 10). The age-2 cohort merged with the adults in November and December, 1985. Growth rate data suggest that a large settlement occurred in Grappler Inlet during the fall of 1984 and in the summer or fall of 1983

Figure 29. Seasonal surface temperature and salinity measurements from January 1984 to December 1985. A, B. Bamfield Inlet. C, D. Grappler Inlet. Horizontal line indicates annual mean.

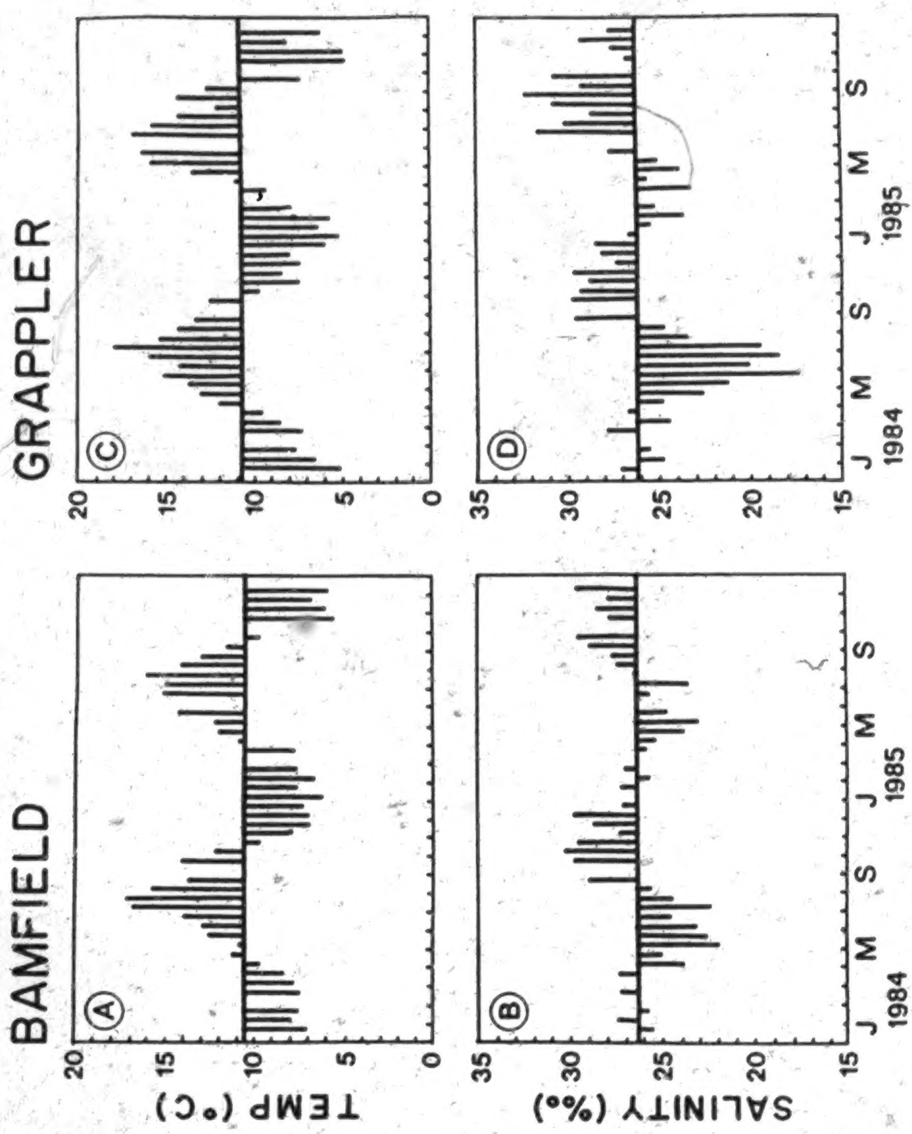

BAMFIELD
GRAPPLER
A
B
C
D
TEMP (°C)
SALINITY (‰)
20
15
10
5
0
35
30
25
20
15
J
M
S
J
M
S
1984
1985

Figure 30. Size-frequency distributions of _Asterina miniata_ from March 1985 to February 1986. Size classes = 0.2 cm. A. Grappler Inlet. B. Bamfield Inlet. Number beneath sample date indicates sample size.

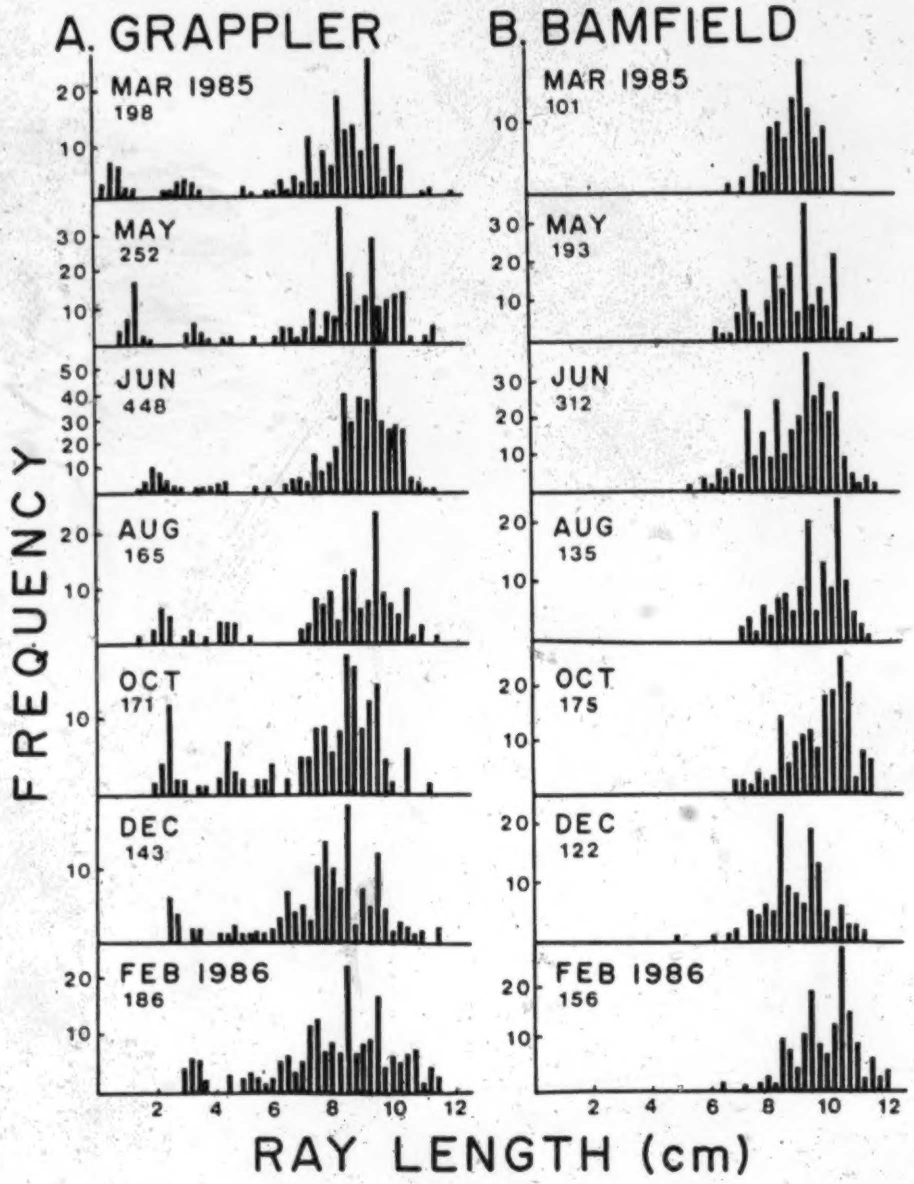

A. GRAPPLER
B. BAMFIELD
MAR 1985
198
101
MAY
252
193
JUN
448
312
AUG
165
135
OCT
171
175
DEC
143
122
FEB 1986
186
156
FREQUENCY
RAY LENGTH (cm)
2
4
6
8
10
12
10
20
30
40
50

TABLE 10

Seasonal estimates of ray length, density and percentage of the monthly population sample for age-1 and age-2 cohorts of *Asterina miniata* at the Grappler Inlet study site. Table entries show ray length values as means, standard deviations are shown in parentheses.

	AGE-1 COHORT			AGE-2 COHORT		
SAMPLE DATE	RAY LENGTH (cm)	COHORT DENSITY (#/5m2)	PERCENT OF SAMPLE (%)	RAY LENGTH (cm)	COHORT DENSITY (#/5m2)	PERCENT OF SAMPLE (%)
MAR 85	0.87 (0.24)	2.00	10.20	3.10 (0.32)	1.30	6.63
MAY	1.35 (0.24)	1.50	11.90	3.77 (0.52)	0.70	5.55
JUN	2.12 (0.34)	1.65	7.36	4.09 (0.30)	0.55	2.45
AUG	2.34 (0.43)	1.70	10.30	4.43 (0.39)	1.40	8.48
OCT	2.47 (0.32)	2.20	12.85	4.90 (0.70)	1.50	8.77
DEC	2.58 (0.71)	1.40	9.72	4.63 (0.37)	0.60	4.17
FEB 86	2.56 (1.11)	1.00	9.14	4.42 (1.55)	1.00	5.38

(Figure 31). Both cohorts of juveniles were absent from the Bamfield Inlet site.

Substantial proportions of the populations of Asterina miniata from both Grappler and Bamfield Inlets were small adults (Figure 30). Skewed size distributions were particularly evident in the June 1985 samples when the histograms included measurements for over 200 individuals. The abundance of small adults in Grappler and Bamfield Inlets suggests that recruitment may have occurred in the past at both sites.

3. Reproductive Activity of Asterina

The Grappler Inlet population of Asterina miniata showed evidence of a long breeding period (Figure 32). Peak gonad index (G.I.) values occurred in mid summer and early fall, whereas low G.I. values occurred in the late fall and winter. These results indicate that most individuals completed spawning by September and October. Mean G.I. values fluctuated between 5 and 11% of total wet-body-weight, and provide evidence for a distinct seasonal cycle (Figure 32). The G.I. frequency distributions were generally bimodal and indicate the co-occurence of gravid and depleted individuals throughout the period of study. Pyloric caeca indices (P.C.I.) fluctuated seasonally between 9 and 15% with a peak value in February and lowest values in May and July (Figure 32). A significant inverse relationship exists between the G.I. and P.C.I values (Kendall's rank correlation,

Figure 31. Growth of post-larval and juvenile *Asterina miniata*. Values shown are ray lengths for post-larvae immediately after metamorphosis in laboratory cultures (▲), ray lengths of 2 juveniles observed in Grappler Inlet prior to the onset of routine sampling (○), and mean ± S.D. for the age-1 cohort estimated from transect surveys (●).

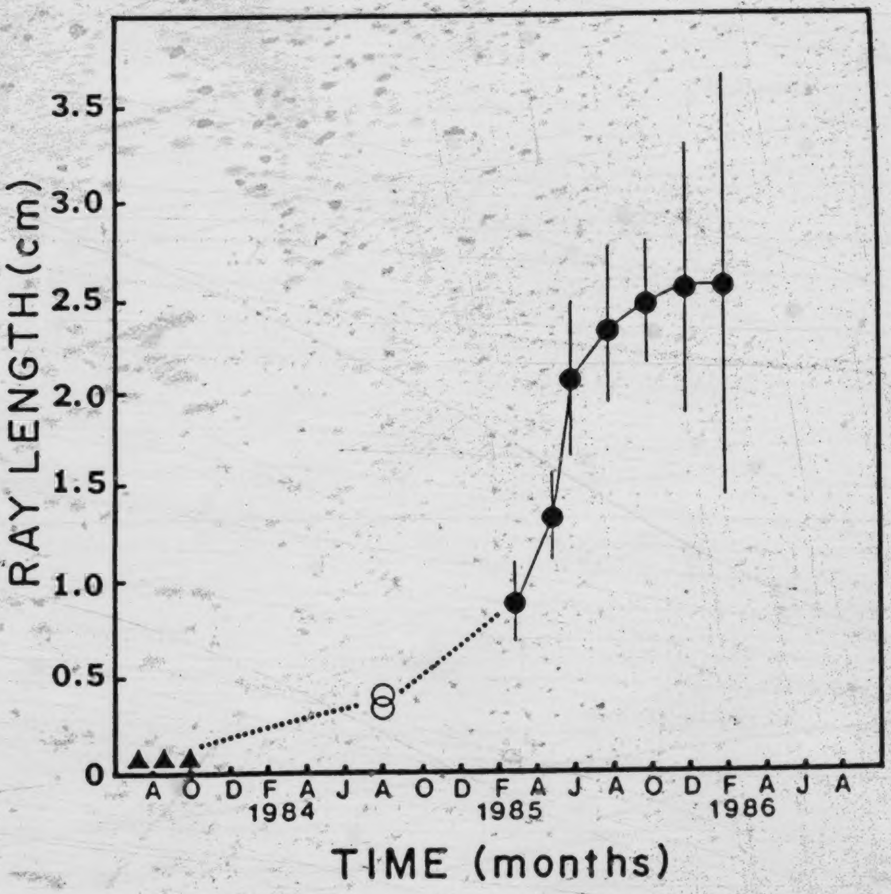
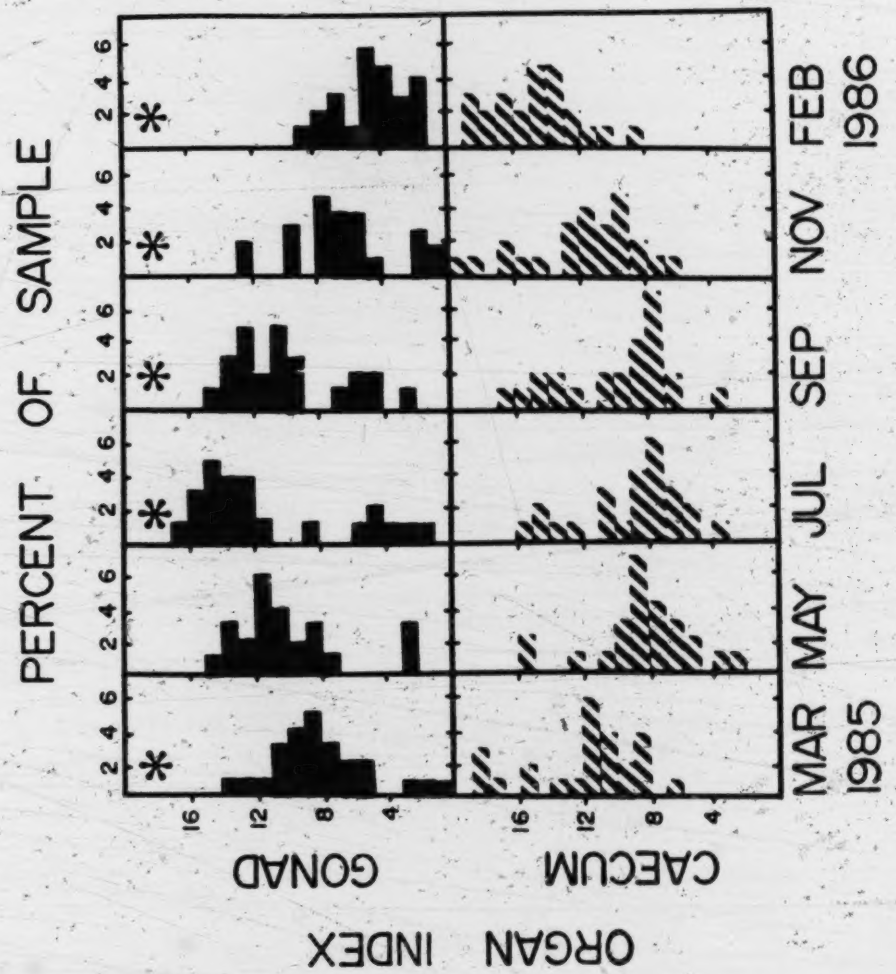

RAY LENGTH (cm)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
A O D F A J A O D F A J A O D F A J A
1984
1985
1986
TIME (months)

Figure 32. Gonad and pyloric caecum indices for *Asterina miniata* from March 1985 to February 1986. Specimens were collected near the Grappler Inlet study site. Histograms show percent of monthly sample; n = 25 individuals per month. Asterisks indicate months when males were observed spawning in the field. The inverse relationship between gonad and pyloric caecum indices is highly significant (Kendall's Rank Correlation, tau = -0.5097, $p < 0.001$).

1.


PERCENT OF SAMPLE
ORGAN INDEX
GONAD
CAECUM
2 4 6
16
12
8
4
*
MAR 1985
MAY
JUL
SEP
NOV
FEB 1986

tau = -0.5097, $p < 0.001$) suggesting that gonadal growth and vitellogenesis occur at the expense of food reserves from the pyloric caecum. Spawning of male _A. miniata_ was observed in the field during all sampling periods except May 1985 (Figure 32).

The planktonic larval period of _Asterina miniata_ is typical for a temperate asteroid with planktotrophic larval development. Fully hydrated ova are 137 ± 6 µm in diameter, and the embryos develop into early feeding bipinnaria larvae after about 4 days (Table 11). Development through the later bipinnaria and settling brachiolaria stages took from 44 to 67 days in cultures maintained between 11 and 15°C. Brachiolariae in substratum selection experiments first completed metamorphosis 79 days after fertilization (Table 11). These observations indicate that metamorphic competence was attained after 8 to 11 wks in the laboratory.

4. _Larval Distribution and Abundance_

Results from stratified plankton tows show that asteroid bipinnaria and brachiolaria larvae were more abundant in surface waters (0-30 m) than in deeper water (Table 12). The occurrence of bipinnaria and brachiolaria larvae differed significantly between depths (Kruskal-Wallis ANOVA, $p < 0.05$). Coefficients of variation became larger with increasing depth for both bipinnariae and brachiolariae, indicating that larval abundances were unpredictable at depths of 60 and 90 m. Bipinnariae were

TABLE 11

Schedule of development for *Asterina miniata* embryos and larvae in laboratory cultures maintained at 11 - 15°C. Times shown are minimum times required to reach a specific stage of development. Cultures were initiated following a natural spawning on May 6, 1985.

DATE	TIME	STAGE OF DEVELOPMENT
MAY 6	0	Insemination
	3 min	Fertilization envelope completed
	2 hrs	First cleavage
	5 hrs	Second cleavage
	7 hrs	Third cleavage
MAY 7	18 hrs	Morula
	26 hrs	Blastula
MAY 8	42 hrs	Hatching
	53 hrs	Gastrula I
MAY 9	71 hrs	Gastrula II
MAY 10	90 hrs	Bipinnaria (early)
MAY 11	128 hrs	Bipinnaria (late)
JUN 19	44 days	Brachiolaria (early)
JUL 6	67 days	Brachiolaria (late)
JUL 18	79 days	First larvae undergo metamorphosis
OCT 30	183 days	Last larvae undergo metamorphosis

TABLE 12

Vertical stratification of asteroid larvae in Trevor Channel (sample site P-1, Figure 28b). Values shown are means (± s.d.). All samples were collected August 20, 1985. C.V. columns indicate coefficients of variation.

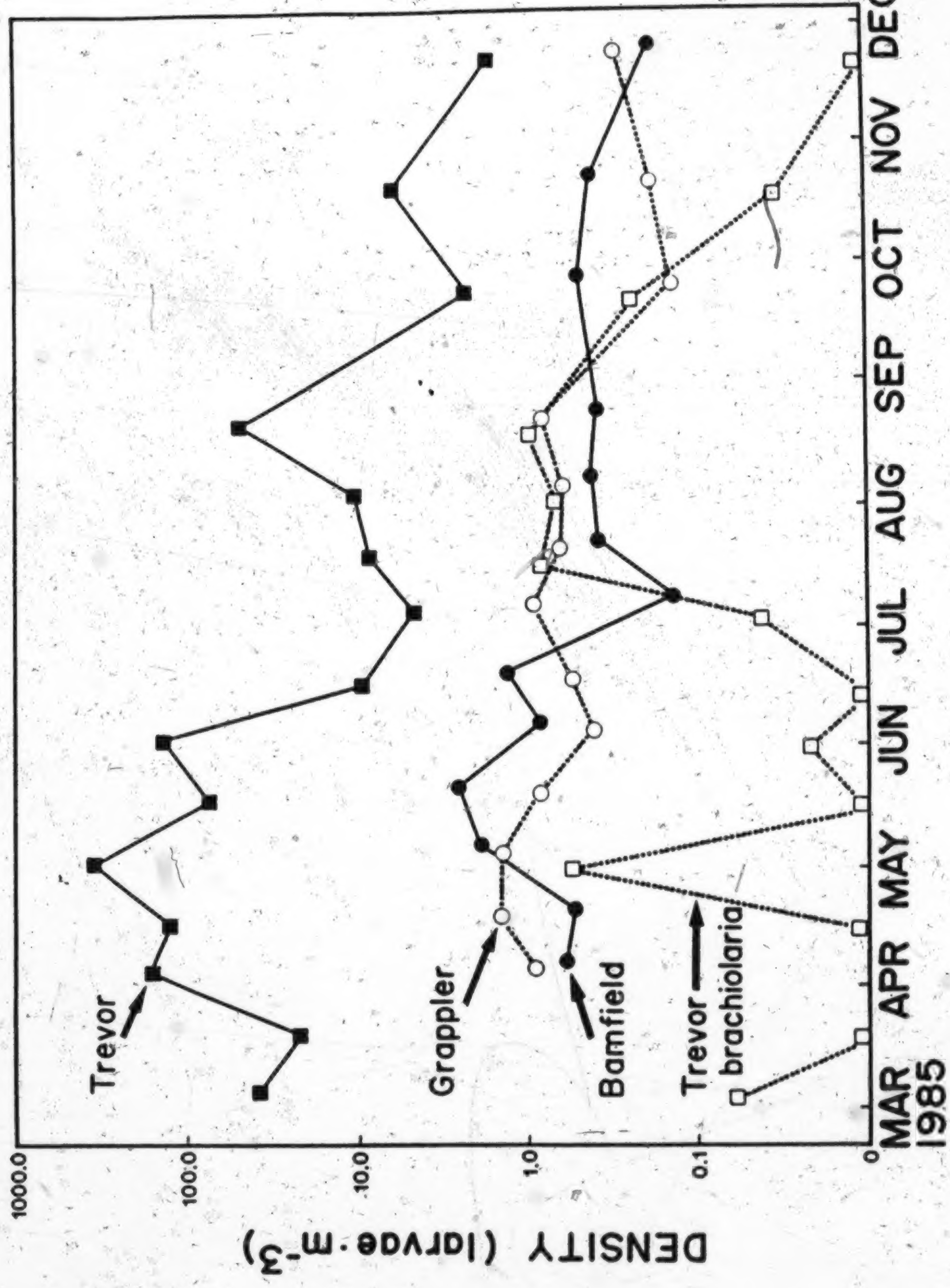
DEPTH STRATUM	# TOWS	SAMPLE VOL. m3	BIPINNARIA #/m3	C.V.	BRACHIOLARIA #/m3	C.V.
0 - 30 m	3	9.47 (1.36)	48.71 (6.97)	0.14	0.91 (0.63)	0.69
30 - 60 m	3	12.90 (2.52)	5.32 (3.89)	0.73	0.04 (0.04)	1.00
60 - 90 m	3	12.37 (1.91)	0.07 (0.12)	1.71	0 (0)	
KRUSKAL-WALLIS ANOVA (H)			7.38		8.27	
p			0.0249		0.0160	

tenfold more abundant than brachiolariae at the 30 and 60 m depths. Few larvae of either stage occurred in samples deeper than 60 m.

Bipinnaria larvae were significantly more abundant in Trevor Channel than in the inlets (Figure 33, Kruskal-Wallis ANOVA, $p < 0.001$). An agreement exists in the seasonal ranking of larval densities between the three sample sites (Kendall's test of concordance, $W = 0.67$, $X^2 = 24.19$, $p < 0.02$). Asteroid bipinnariae were most abundant in the spring and early summer months (Figure 33). In contrast, few brachiolariae were collected in the spring, and they reached their greatest densities during July and August. No brachiolaria larvae occurred in plankton tows collected in Bamfield or Grappler Inlet in 1985. However, two spinulosid brachiolaria larvae were identified from a series of plankton tows collected in Grappler Inlet in June 1986. No larvae were sampled in June 1986 at Bamfield Inlet.

Two lines of evidence suggest that similar numbers of asteroid larvae are transported into Bamfield and Grappler Inlets from Trevor Channel. First, pooled rank counts of bipinnariae showed no significant differences in the numbers of larvae in the inlets during the late summer when larvae are expected to enter the inlets prior to settlement (Jul - Oct, Mann Whitney 2 Sample Test, $Z = 0.8177$; $p = 0.4135$). Second, ranked counts of bipinnariae showed that larvae were equally abundant in Bamfield and Grappler

Figure 33. Seasonal abundance of asteroid larvae at 3 zooplankton sample sites in 1985. Values show density of bipinnaria larvae in Trevor Channel (■), Bamfield Inlet (●) and Grappler Inlet (○). Densities of brachiolaria larvae are shown in Trevor Channel (□). Values are mean larvae·m^{-3}, $n = 3$ tows per sample date.


DENSITY (larvae·m^{-3})
1000.0
100.0
10.0
1.0
0.1
0
MAR
1985
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Trevor
Grappler
Bamfield
Trevor
brachiolaria

Inlets when densities of larvae were compared over an entire year ($Z = 0.1206$, $p = 0.9039$). The supply of planktonic larvae is apparently similar in Bamfield and Grappler Inlets due to a wind-driven advective transport mechanism that moves surface waters into the inlets from Trevor Channel. Consequently, spatial differences in the recruitment of *Asterina miniata* between Bamfield and Grappler Inlets cannot be attributed to differences in the spatial distribution of larvae.

5. *Larval Substratum Selection*

Settlement experiments in which larvae were offered a choice of substrata showed that the distribution of metamorphosed *Asterina miniata* was significantly different from a uniform distribution after incubation periods of 48 hrs ($X^2 = 27.1374$, $p = 0.0074$) and 72 hrs ($X^2 = 45.8608$, $p = 5.6 \times 10^{-5}$; Table 13). In contrast, counts of metamorphosed post-larvae from assays conducted after 24 hrs suggested indiscriminant site selection ($X^2 = 12.8771$, $p = 0.30$). Since metamorphosis of *A. miniata* brachiolariae requires 36 to 50 hrs to complete, patterns of site selection based on 24 hr counts may be biased in favor of larvae that exhibit low discrimination and complete metamorphosis rapidly.

Although *Asterina miniata* post-larvae occurred on 6 of 8 substrata, the number of larvae that completed metamorphosis on sediments from Grappler Inlet was significantly greater than that expected for uniform

TABLE 13

Metamorphosis of *Asterina miniata* in the multiple substratum settlement experiment. Table entries show the mean (± s.d.) number of post-larvae observed on various substrata after incubation periods of 48 and 72 hours. P values show probability levels for Mann-Whitney tests against the number of post-larvae expected for uniform settlement. Brachiolaria larvae were 79 days old at the beginning of the experiments.

SUBSTRATUM	n	NUMBER OF METAMORPHOSED POST-LARVAE			
		48 HRS	p	72 HRS	p
Glass Fragment:					
Clean	3	0.00	0.0468	0.00	0.0468
Aged	3	3.67 (3.21)	0.8802	4.33 (2.08)	0.2682
Shell Fragment:					
Tresus nuttalli	3	3.00 (1.00)	0.2668	3.33 (0.58)	0.0816
Rock Fragment:					
Aged	3	3.67 (2.08)	0.3075	3.33 (1.53)	0.4076
Soft-Sediments:					
Grappler Inlet	3	5.67 (1.15)	0.0160	6.33 (1.15)	0.0153
Rhodophyta:					
Lithothamnion sp.	3	1.00 (1.00)	0.2331	1.33 (0.58)	0.1029
Gracillaria pacifica	3	0.00	0.0468	0.00	0.0468
Chlorophyta:					
Ulva sp.	3	0.00	0.0468	0.33 (0.58)	0.0508
EXPECTED VALUE FOR UNIFORM SETTLEMENT		2.13		2.38	

settlement (Table 13). In contrast, the numbers of post-larvae on Ulva sp., Gracillaria pacifica and clean glass were significantly less than expected. These results indicate that A. miniata brachiolariae settle and complete metamorphosis non-selectively on substrata that are covered with a surface film, and that sediments offer a preferred site for metamorphosis.

Settlement experiments in which larvae were offered only a single substratum showed greater metamorphosis in treatments containing sediments collected from Bamfield and Grappler Inlets compared with treatments containing sediments from outside the inlets (Figure 34ab, $X^2 = 19.27$, $p < 0.001$; and Table 14). The number of Asterina miniata post-larvae in treatments containing sediment from Grappler Inlet was greater than that in treatments containing sediment from Bamfield Inlet (Figure 34), and sediment from Grappler Inlet appeared to be more attractive to settling larvae than sediment from Bamfield Inlet. However, the difference was only marginally significant (p values from 0.041 to 0.059, Table 14). To reduce the possibility of a Type II error (viz. erroneous acceptance of the null hypothesis that the substrata from Bamfield and Grappler Inlets did not differ as a cue for metamorphosis), the results of substratum selection experiments 1 and 2 were combined (Sokal and Rohlf, 1981). Substratum selection differed significantly when the results from Mann-Whitney U-tests were analyzed together

Figure 34. Metamorphosis of Asterina miniata in single substratum experiments. A. 84 day old larvae, 50 larvae·trial^{-1}. B. 91 day old larvae, 20 larvae·trial^{-1}. Values show % metamorphosis in treatments containing sediments collected from Grappler Inlet (○), Bamfield Inlet (●) and Aguilar Point (◆).

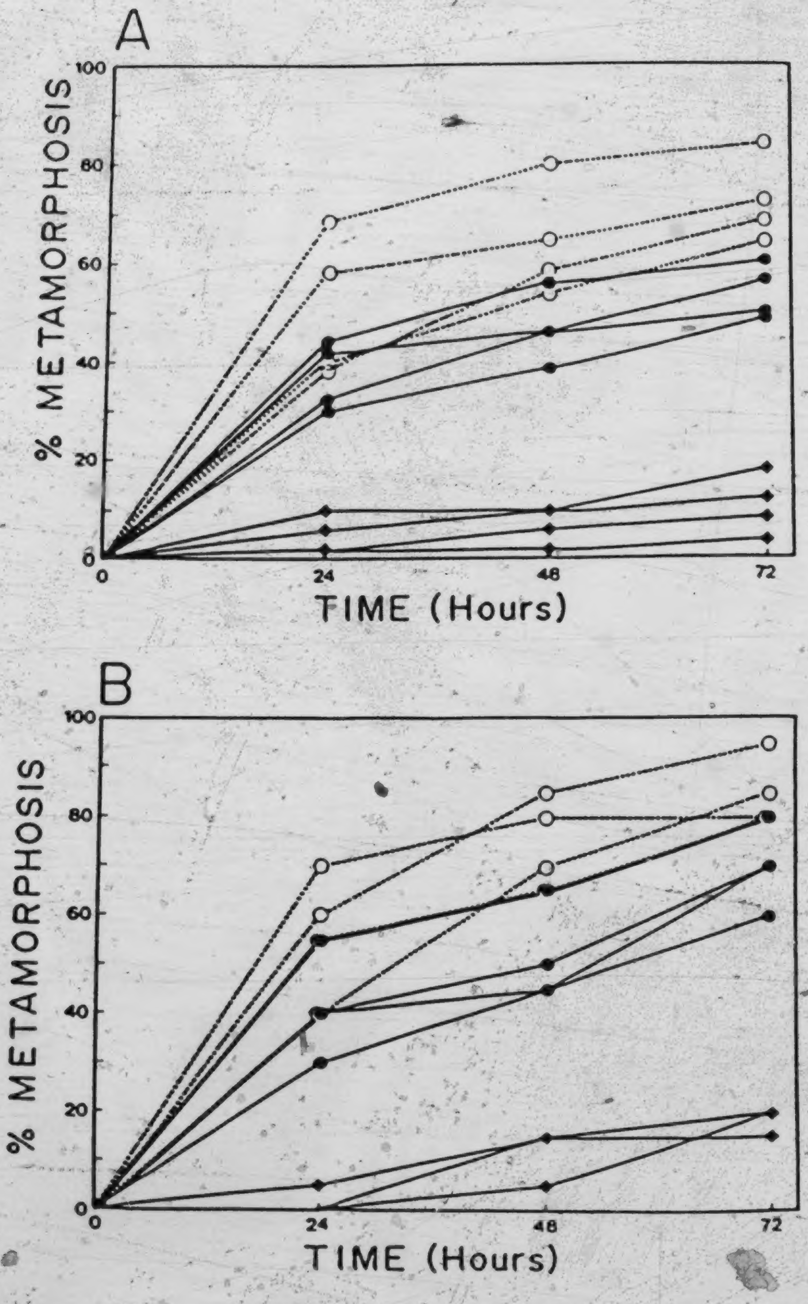

A
100
80
60
40
20
0
% METAMORPHOSIS
0
24
48
72
TIME (Hours)
B
100
80
60
40
20
0
% METAMORPHOSIS
0
24
48
72
TIME (Hours)

TABLE 14

Metamorphosis of *Asterina miniata* in single substratum experiments. Values show Mann-Whitney U-test statistics and probability levels in two sample comparisons of the number of post-larvae observed on Bamfield and Grappler Inlet sediments. The results of Mann-Whitney U-tests are also shown for a comparison of the number of *A. miniata* post-larvae observed on sediments collected from the Inlets (pooled data) and sediments collected outside the Inlets (see Figure 28b). Combined test column indicates chi-square values and probability levels obtained by combining probabilities from Mann-Whitney U-tests.

TIME OF COMPARISON		SETTLEMENT EXPERIMENT		COMBINED TEST
		#1	#2	#1 AND #2
BAMFIELD VS. GRAPPLER INLET SEDIMENTS:				
24 HOURS	U	1.0104	1.4884	Chi Sqr = 6.3075
	p	0.3123	0.1367	p < 0.5000
48 HOURS	U	1.8877	2.0452	Chi Sqr = 12.0552
	p	0.0591	0.0408	p < 0.0250
72 HOURS	U	1.9349	1.9349	Chi Sqr = 11.7498
	p	0.0530	0.0530	p < 0.0250
INLET SEDIMENTS VS. OUTSIDE SEDIMENTS:				
48 HOURS	U	2.6325	2.6654	Chi Sqr = 19.2684
	p	0.0085	0.0077	p < 0.0010

after 48 hrs (Table 14, $X^2 = 12.05$, $p < 0.025$) and 72 hrs ($X^2 = 11.75$, $p < 0.025$). Taken collectively, these results indicate that sediments from Grappler Inlet are more attractive as sites for settlement and metamorphosis of A. miniata brachiolariae than sediments from Bamfield Inlet.

Results from a final set of settlement experiments showed that aged-sediments induced significantly greater numbers of Asterina miniata to complete metamorphosis compared with fresh-sediments (Mann-Whitney test, $p < 0.05$; Table 15). Post-larvae were 2 - 4 times more abundant in the aged-sediment treatments than in treatments containing fresh-sediments. Presumably, aged sediments developed a surface film associated with bacteria and other microorganisms, although they were not examined specifically for bacteria. These results provide further evidence that the substratum selection response of A. miniata brachiolariae is independent of microtopographical features of the substratum including sediment grain size and texture.

6. Predation upon Larvae by Benthic Suspension Feeders

Transect surveys conducted in June 1985 showed marked differences in the abundance of benthic suspension feeders between Bamfield and Grappler Inlets (Table 16). The solitary phelebobranch ascidian, Corella willmeriana, averaged 254 individuals m^{-2} in Bamfield Inlet, but individuals were nearly absent in Grappler Inlet.

TABLE 15

Metamorphosis of *Asterina miniata* in the sediment aging experiment. Table entries show the number of *A. miniata* post-larvae on fresh and aged sediments collected outside the inlets at Aguilar Point (see Figure 28b). Values shown are means (± s.d.). The results from Mann-Whitney U-tests are also shown along with their associated probability levels.

AGUILAR POINT SEDIMENT TREATMENTS	n	INCUBATION PERIOD (Hours)		
		24	48	72
FRESH:	4	1.25 (0.50)	2.75 (1.26)	4.00 (0.82)
AGED: 9 days in running seawater	4	5.00 (1.54)	6.50 (1.73)	8.75 (2.36)
CONTROL: no sediment	4	0.00	0.25 (0.50)	0.75 (0.96)
MANN-WHITNEY U-TEST: FRESH VS. AGED SEDIMENTS				
U		2.2468	2.0578	2.1913
p		0.0247	0.0396	0.0284

TABLE 16

Densities of benthic suspension feeders in Bamfield and Grappler Inlets. Benthic transects were surveyed in June, 1985. Table entries show the mean number of individuals or colonies per square meter. Standard deviations are shown in parentheses. IND = individual; COL = Colony; PRESENT = Species present but did not occur along benthic transect line.

SPECIES	UNITS	BAMFIELD INLET		GRAPPLER INLET	
		mean	(s.d.)	mean	(s.d.)
Corella willmeriana	IND	253.8	(158.7)	0.3	(1.5)
Pachycerianthus fimbriatus	IND	6.7	(3.5)	13.2	(4.3)
Protothaca staminea	IND	2.9	(6.3)	1.3	(3.8)
Tubularia crocea	COL	0.9	(1.7)	0.4	(1.2)
Polyorchis penicillatus	IND	0.8	(2.2)	0.1	(0.7)
Metridium senile	IND	0.4	(1.2)	0.3	(1.0)
Tresus nuttalli	IND	0.1	(0.7)	0.5	(1.4)
Bugula pacifica	COL	0.1	(0.7)	0.4	(1.2)
Obelia frondosa	COL	PRESENT		0.3	(1.0)
Ptilosarcus gurneyi	IND	0.1	(0.7)		
Phoronis vancouveriensis	COL			0.1	(0.7)
Saxidomus dalli	IND	PRESENT		PRESENT	

Conversely, individuals of the tube-dwelling cerianthid anemone, *Pachycerianthus fimbriatus*, were significantly more abundant in Grappler Inlet than in Bamfield Inlet (Mann-Whitney 2 sample test, $Z = 2.85$, $p = 0.0050$). Individuals of *C. willmeriana* exhibited a dramatic seasonal cycle of abundance in Bamfield Inlet (Figure 35a; $p < 0.001$) where high densities occurred during the summer months from June through October. In contrast, there were no seasonal differences in the abundance of *P. fimbriatus* in either Bamfield Inlet (Figure 35b; Kruskal-Wallis ANOVA; $p = 0.69$) or Grappler Inlet ($p = 0.17$). With the exception of the bivalve, *Protothaca staminea*, densities of other suspension feeders were low in both inlets (Table 16). The hydromedusan, *Polyorchis penicillatus*, and the anthozoan, *Metridium senile*, were included in the survey because these cnidarians are capable of microphagous predation upon demersal zooplankton (Purcell, 1977; Arkett, 1984; Sebens and Koehl, 1984). These results suggest that the heterogeneous distribution of benthic suspension feeders may be one factor determining differential recruitment of *Asterina miniata* between Bamfield and Grappler Inlets.

a. *Analysis of Gut Contents*

Analysis of gut contents showed that a large proportion of the prey items of both *Corella willmeriana* and *Pachycerianthus fimbriatus* fall between 75 and 250 µm in length (Figure 36). Prey items greater than 375 µm are seldom ingested by *C. willmeriana*, but a few prey items

Figure 35. Seasonal densities of benthic suspension feeders in Bamfield (□) and Grappler (■) Inlets in 1985.

A. *Corella willmeriana*. Values in parentheses show density in Grappler Inlet in June and August. *C. willmeriana* were absent during all other sample periods.

B. *Pachycerianthus fimbriatus*. Histograms show mean, error bars indicate ± S.D.

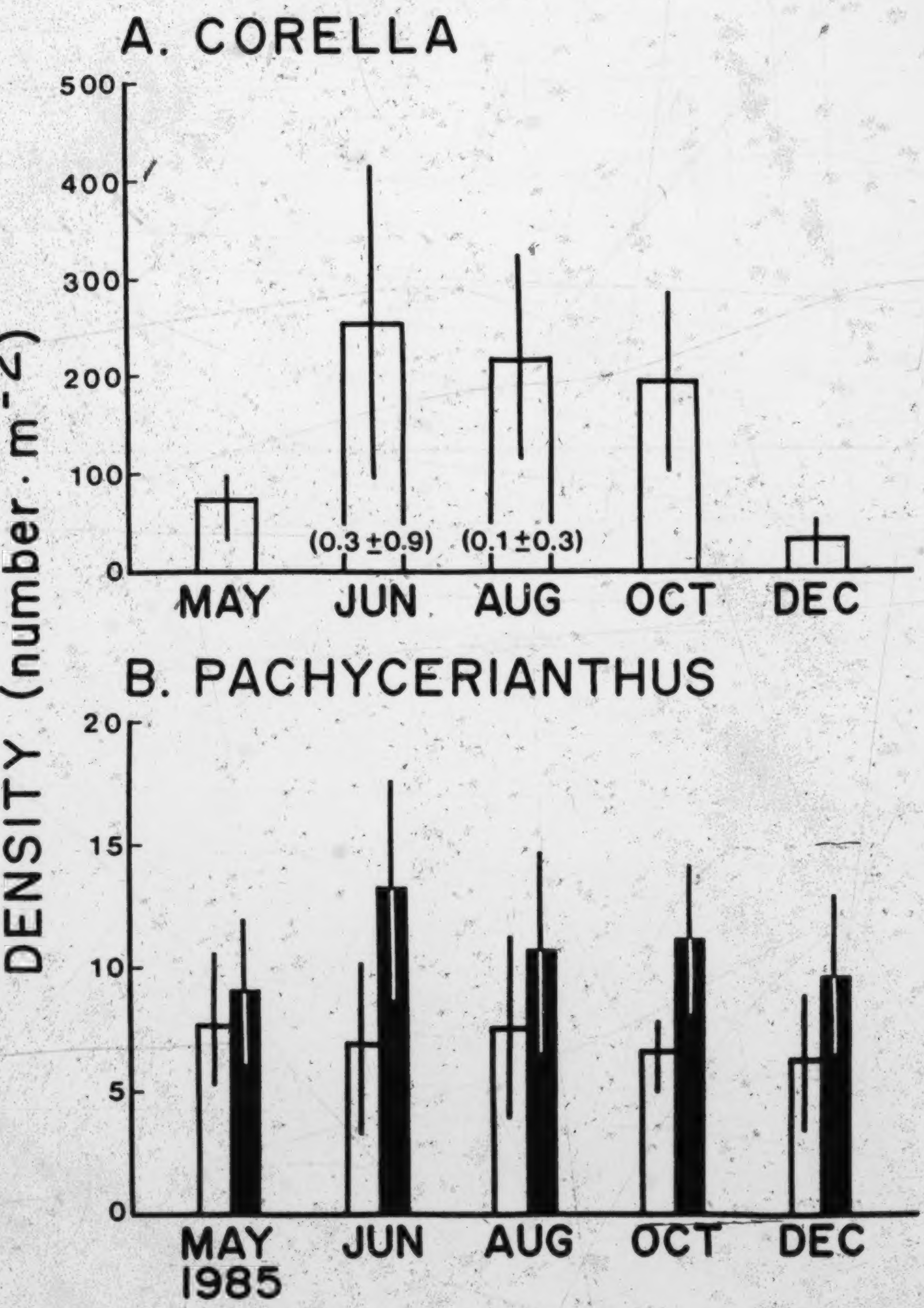
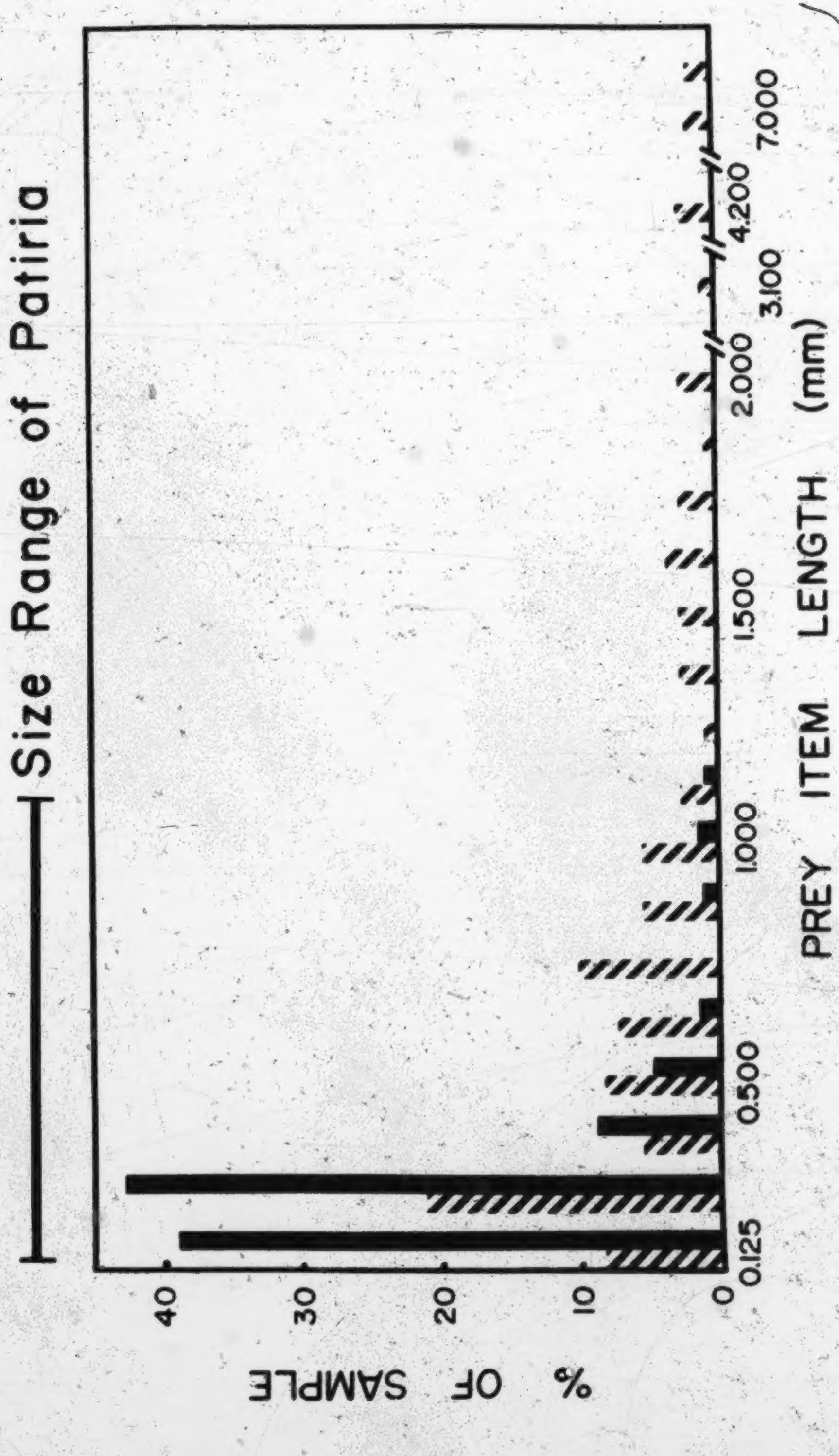

A. CORELLA
500
400
300
200
100
0
(0.3 ±0.9)
(0.1 ±0.3)
MAY
JUN
AUG
OCT
DEC
DENSITY (number · m^{-2})
B. PACHYCERIANTHUS
20
15
10
5
0
MAY
1985
JUN
AUG
OCT
DEC

Figure 36. Size distribution of prey items recovered from gut contents of Corella willmeriana (■, 27 individuals, n = 312 prey items) and Pachycerianthus fimbriatus (▧, 17 individuals, n = 109 prey items). Figure also shows overlapping size range of Asterina miniata embryos and larvae (see Table 9).


Size Range of Patiria
% OF SAMPLE
40
30
20
10
0
0.125
0.500
1.000
1.500
2.000
3.100
4.200
7.000
PREY ITEM LENGTH (mm)

with lengths up to 1 mm were recovered. Most prey items recovered from the gastrovascular cavity of *P. fimbriatus* fall between 125 µm and 2 mm in length. The majority of small prey items were diatoms, invertebrate embryos and nauplii; the larger prey items included copepods, barnacle cyprids and small polychaetes. The size range of *Asterina miniata* embryos and larvae overlaps with the range of prey items consumed by *P. fimbriatus* and *C. willmeriana* (see Table 9, Figure 36). Consequently, it was inferred that natural populations of these suspension feeders were capable of capturing settling *A. miniata* larvae in the field.

b. Laboratory Predation Experiments

Differences in the susceptibility of *Asterina miniata* embryos and larvae to predation were highly significant in feeding experiments conducted with *Pachycerianthus fimbriatus* (Figure 37, Kruskal Wallis ANOVA, $H = 19.93$, $p = 0.0013$) and *Corella willmeriana* ($H = 29.95$, $p < 0.001$). The percentage of early prey stages captured by *P. fimbriatus* (pooled mean = 16.5%) was significantly less than capture frequencies for *A. miniata* gastrulae (29%) and brachiolariae (30%; Student-Newman-Keuls tests, Table 17, Figure 37a). Low capture frequencies observed for bipinnariae (19%) were inconsistent with the trend toward increased susceptibility of late-stage larvae. An opposite trend, toward decreased susceptibility during development, was evident during feeding experiments conducted with

Figure 37. Mortality of various developmental stages of *Asterina miniata* during single-stage feeding experiments with benthic suspension feeders. A. Predation by *Pachycerianthus fimbriatus*. B. Predation by *Corella willmeriana*. Values shown are means, error bars indicate ± S.D. Numbers above error bars indicate sample sizes. Solid bars show capture frequencies in predator treatments; open bars indicate loss of prey in controls. The developmental stages of *A. miniata* are described in Table 9.

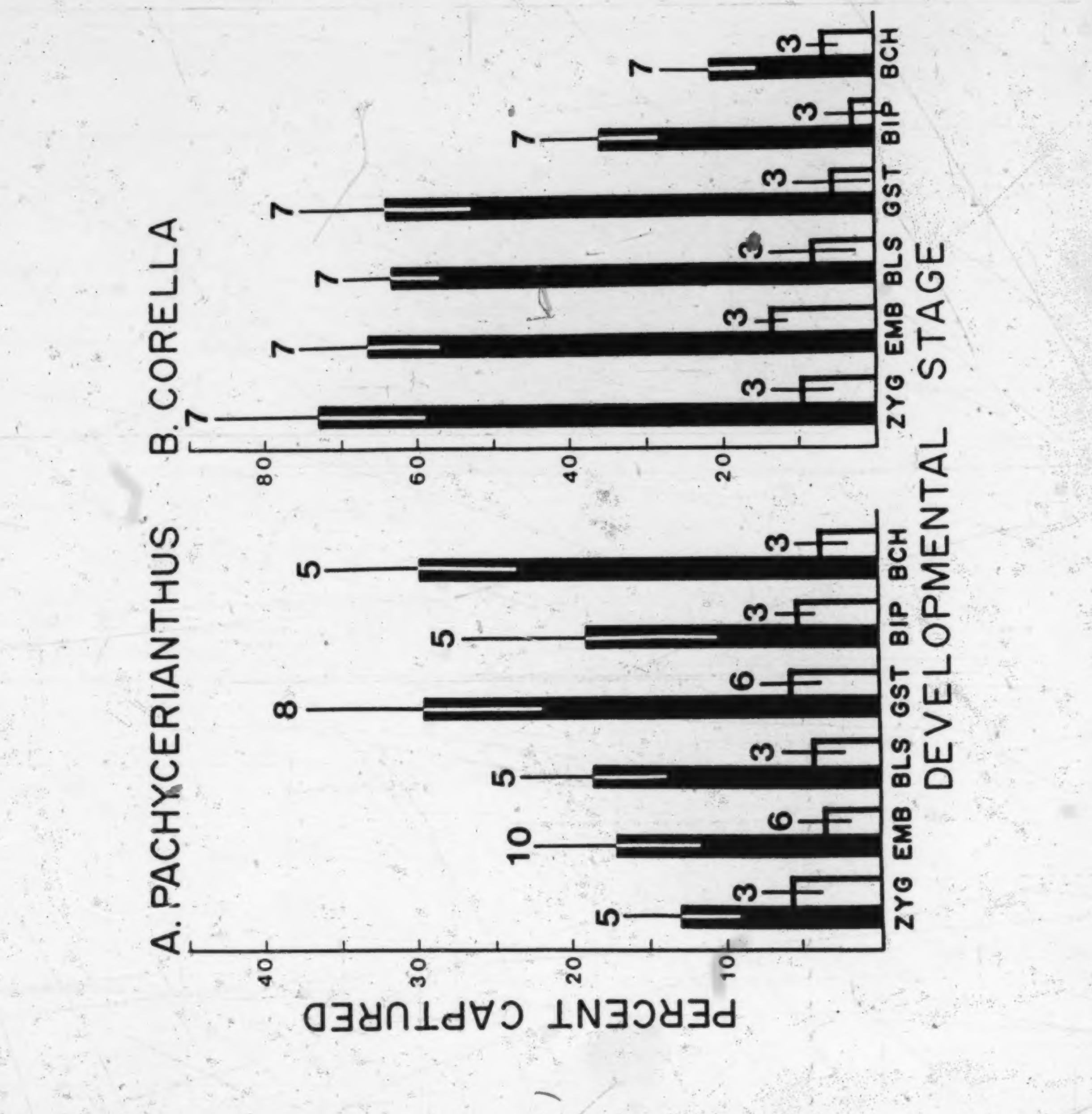

A. PACHYCERIANTHUS
B. CORELLA
PERCENT CAPTURED
DEVELOPMENTAL STAGE
10
20
30
40
20
40
60
80
ZYG
EMB
BLS
GST
BIP
BCH
5
3
10
6
5
3
8
6
5
3
5
3
7
3
7
3
7
3
7
3
7
3
7
3

TABLE 17

Summary of Student-Newman-Keuls tests of differences in capture frequencies between developmental stages of *Asterina miniata*. Upper-right region of table shows the significance levels of SNK tests for predation experiments conducted with *Pachycerianthus fimbriatus*. Lower-left region of table shows the significance levels of SNK tests for predation experiments conducted with *Corella willmeriana*.

		Pachycerianthus: DEVELOPMENT STAGE					
Corella:		ZYG	EMB	BLS	GST	BIP	BCH
DEVELOPMENT STAGE	ZYG		n.s.	n.s.	0.01	n.s.	0.05
	EMB	n.s.		n.s.	0.01	n.s.	0.05
	BLS	n.s.	n.s.		0.05	n.s.	n.s.
	GST	n.s.	n.s.	n.s.		0.05	n.s.
	BIP	0.01	0.01	0.01	0.01		n.s.
	BCH	0.01	0.01	0.01	0.01	0.05	

C. willmeriana (Figure 37b). Capture frequencies for embryonic and early larval stages (pooled mean = 67%) were significantly greater than for late-stage larvae such as bipinnariae (36%) and brachiolariae (22%, see Table 17). Losses of larvae were low in all control treatments and indicated significant predation effects for all developmental stages of *A. miniata*. Overall capture frequencies (all developmental stages) averaged 21 ± 9% ($n = 38$) for *P. fimbriatus* compared with a pooled mean of 54 ± 21% ($n = 42$) for *C. willmeriana*.

There were significant density effects in the predation rates of *Corella willmeriana* and *Pachycerianthus fimbriatus* (Figure 38, Table 18, ANOVA, $p < 0.001$). Stage-specific differences in the susceptibility of *Asterina miniata* embryos and larvae (Figure 37) were also evident in the shapes of functional response curves (Figure 38). In *C. willmeriana*, the slope of the functional response curve for non-motile embryos was significantly greater than the slope for swimming bipinnaria larvae ($t = 3.46$; $p < 0.01$), indicating higher rates of predation upon embryos compared with bipinnaria larvae. The functional response curve for *C. willmeriana* shows evidence of saturation (Holling, 1966; Type II) for embryos and larvae at initial prey densities between 100 and 200 prey liter^{-1} (Figure 38a). In contrast, the functional response curves for *P. fimbriatus* were linear (embryos: Holling Type I, Figure 38b) or showed evidence of the early region of a sigmoidal curve

Figure 38. Partial functional responses of suspension feeders to differences in the density of *Asterina miniata* prey stages. A. Predation by *Corella willmeriana*. B. Predation by *Pachycerianthus fimbriatus*. Values show the results of predation experiments (n=3 trials per initial prey density) upon *A. miniata* embryos (○) and bipinnariae (●). Solid lines show least squares regression fit to functional response data for embryos (*C. willmeriana*, $r^2 = 0.7986$; *P. fimbriatus*, $r^2 = 0.9384$) and bipinnaria larvae (*C. willmeriana*, $r^2 = 0.7556$; *P. fimbriatus*, $r^2 = 0.9369$)

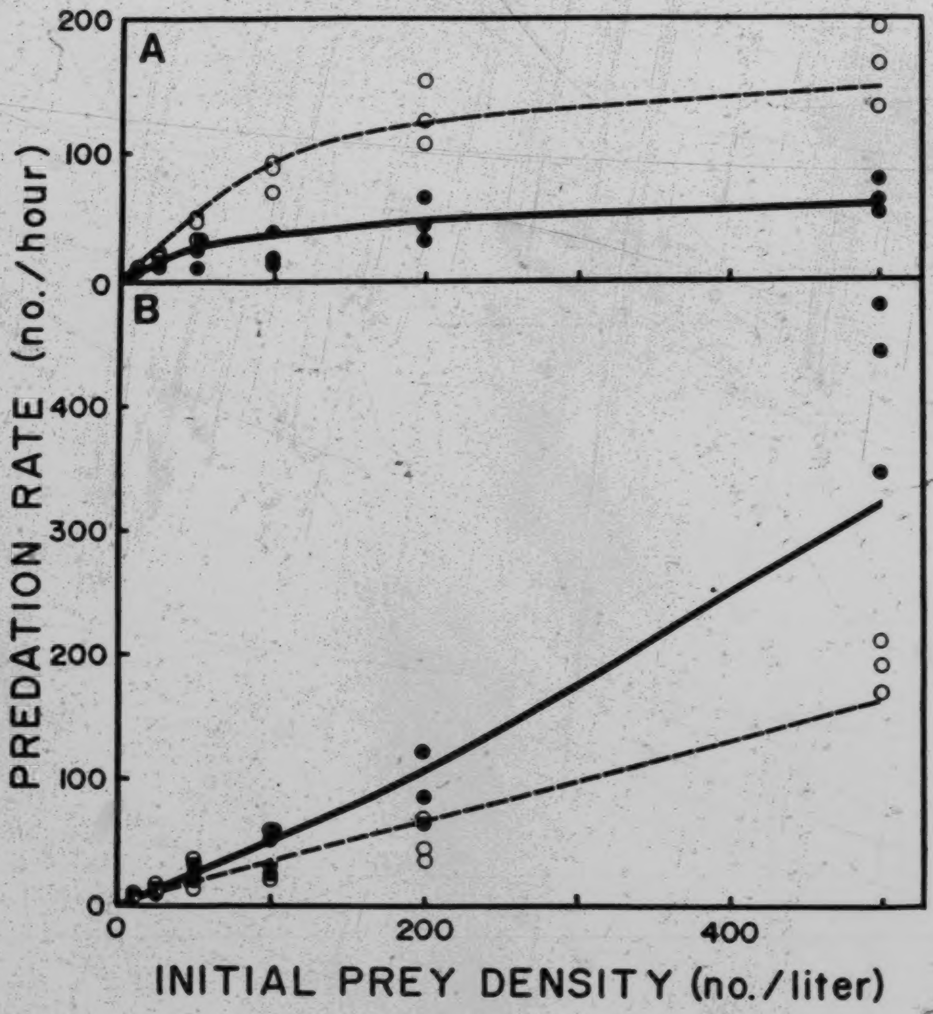

A
B
PREDATION RATE (no./hour)
200
100
0
400
300
200
100
0
0
200
400
INITIAL PREY DENSITY (no./liter)

TABLE 18

Results of single-factor ANOVA tests of the effects of prey density on predation rates upon *Asterina* embryos and larvae by *Corella* and *Pachycerianthus* during functional response feeding experiments.

PREDATOR SPECIES	PREY STAGE	SOURCE	SS	DF	MS	F-RATIO	P
Corella:							
	EMBRYOS						
		Density	61615.11	5	12323.02	44.93	p<0.001
		Error	3291.33	12	274.28		
	BIPINNARIAE						
		Density	7159.78	5	1431.96	11.05	p<0.001
		Error	1555.33	12	129.61		
Pachycerianthus:							
	EMBRYOS						
		Density	73516.28	5	14703.26	69.32	p<0.001
		Error	2545.33	12	212.11		
	BIPINNARIAE						
		Density	391611.6	5	78322.32	78.12	p<0.001
		Error	12030.67	12	1002.56		

(bipinnariae: Holling Type III). The slope of the predation rate curve for swimming bipinnaria larvae was significantly greater than the predation rate curve for embryos ($t = 12.38$; $p < 0.001$).

Differences in the efficiency of filtration by *Corella willmeriana* and *Pachycerianthus fimbriatus* were substantial during feeding experiments conducted with different developmental stages of *Asterina miniata* (Table 19). For example, *C. willmeriana* captured 92% of the embryos and 87% of the bipinnariae that entered the parabolic volume of seawater immediately upstream from the incurrent siphon. In contrast, *P. fimbriatus* captured only 7% of the embryos and 11% of the bipinnariae that passed through the crown of tentacles. These results are consistent with differences in embryo and larval susceptibility observed during feeding experiments (Figures 37 and 38). Taken collectively, laboratory experiments suggest that the feeding activities of *C. willmeriana* and *P. fimbriatus* may have different qualitative and quantitative effects on populations of settling *A. miniata* larvae.

Stage-specific differences in predation rates (Figures 37 and 38) reflect not only differences in the susceptibility of *Asterina miniata* embryos and larvae but also differences in the modes of feeding utilized by *Corella willmeriana* and *Pachycerianthus fimbriatus* to capture prey. Saturation characteristics illustrated by the functional response curve in *C. willmeriana* (Figure 38a)

TABLE 19

Filtration efficiencies of *Corella* and *Pachycerianthus* during flow tank feeding experiments. Encounter value indicates number of *Asterina* embryos or bipinnaria larvae whose streamline passed within the feeding current paraboloid of *Corella* or tentacle sphere of *Pachycerianthus*. Flume velocity = 4.9 mm/s.

PREDATOR SPECIES	PREY STAGE	# PREY ENCOUNTERED	# PREY CAPTURED	FILTRATION EFFICIENCY
Corella willmeriana	EMB	147	136	92.52 %
	BIP	71	62	87.32 %
Pachycerianthus fimbriatus	EMB	86	5	6.81 %
	BIP	55	6	10.91 %

appear to be related to a density-dependent decrease in the filtration efficiency of the branchial basket. After A. miniata embryos or larvae pass through the incurrent siphon, they become trapped in mucus and accumulate against the wall of the branchial basket where they interfere with the passage of currents through the stigmata (Figure 39). In contrast, P. fimbriatus captures A. miniata larvae with nematocysts and mucus located along the marginal tentacles (Figure 40). The tentacles of P. fimbriatus exhibited a characteristic feeding response (withdrawal toward the labial tentacles) after they were contacted by swimming A. miniata larvae. Microscopic examinations of several A. miniata bipinnariae recovered at the end of feeding experiments revealed the presence of stenotele nematocysts embedded in the larval epidermis (Figure 40c). Since the fate of these larvae was not followed, the long-term effects of tentacle contact and nematocyst penetration are unknown.

c. Predator Encounter Rates

The relative importance of predation upon settling Asterina miniata larvae was compared between Bamfield and Grappler Inlets with a random walk model (Roberts, 1975). The aerosol filtration equations used in the model were originally developed by Pich (1966), and later adapted for benthic suspension feeding invertebrates by Rubenstein and Koehl (1977) and LaBarbara (1984). The dimensionless ratio (N_{mf}) that expresses the frequency of particle capture by

Figure 39. Transverse paraffin section through the branchial basket of Corella willmeriana. The specimen was fixed after the termination of a functional response feeding experiment. The section shows several Asterina miniata ova (O) retained within the branchial basket (BB). Arrows indicate the direction of water flow during feeding. S = stigmata, AT = atrium, TU = tunic. Scale bar = 200 µm.

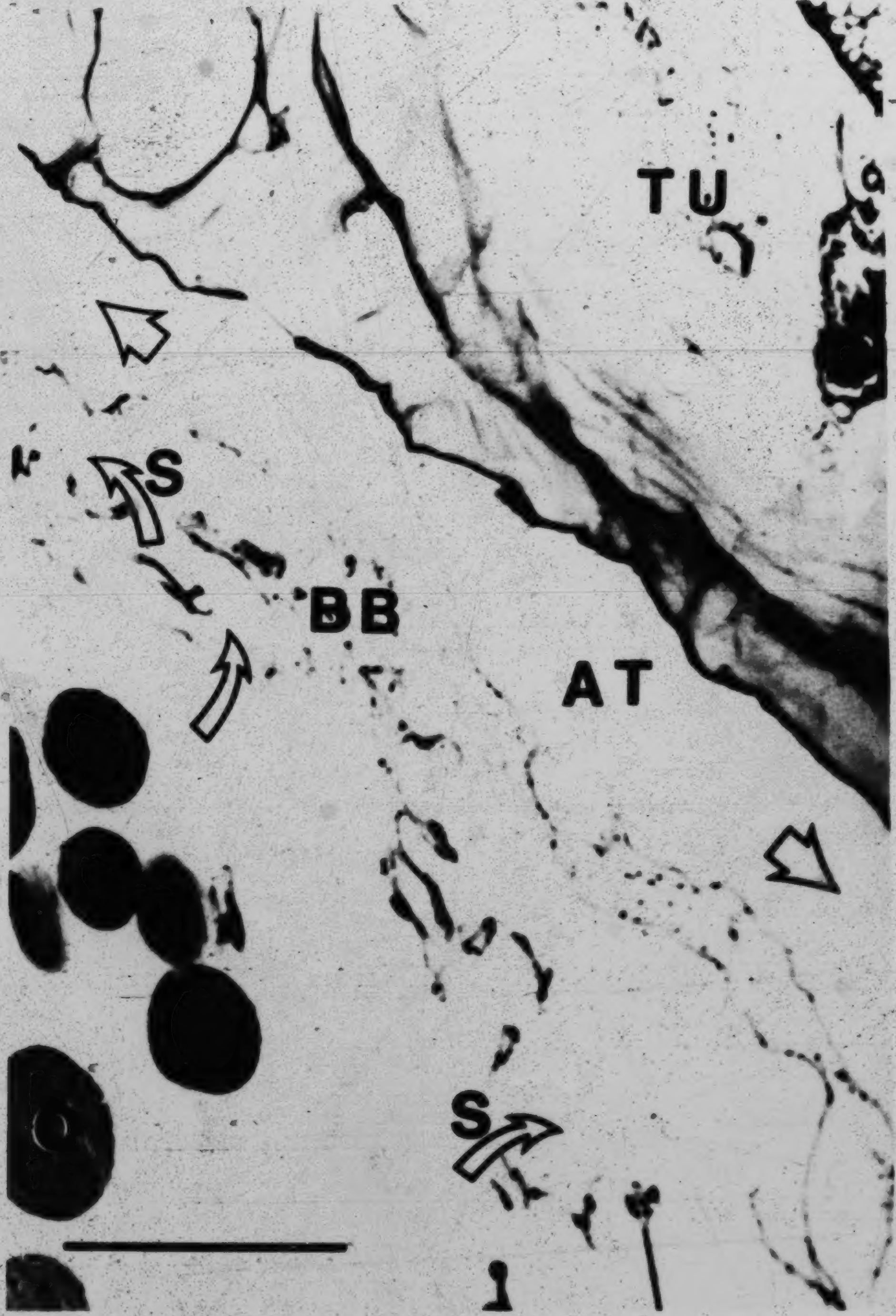
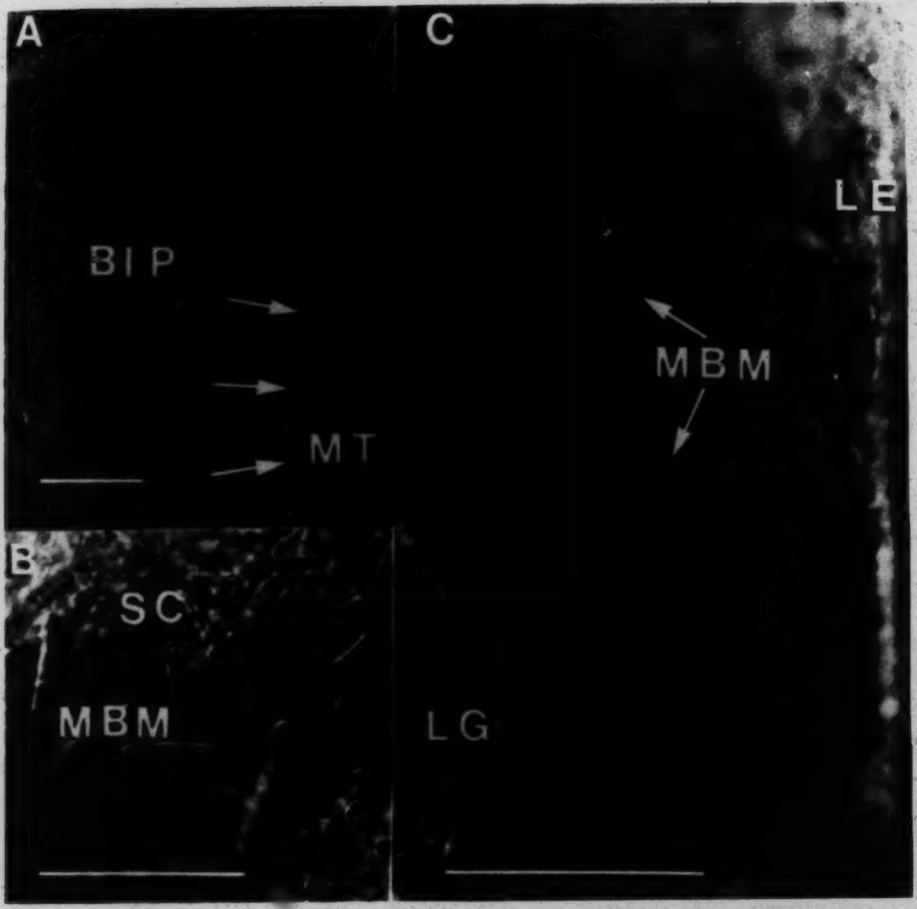

TU
S
BB
AT
S
1

Figure 40. Capture of *Asterina miniata* bipinnariae by marginal tentacles of *Pachycerianthus fimbriatus*. A. Bipinnaria larvae affixed by nematocysts and mucus to a marginal tentacle. Arrows indicate points of contact between larval epidermis and tentacle. B. Undischarged nematocysts within a marginal tentacle. C. Discharged nematocysts embedded in the epidermis of a *A. miniata* bipinnaria larva. Arrows indicate discharged nematocysts. BIP = *A. miniata* bipinnaria, MT = *P. fimbriatus* marginal tentacle, SC = spirocyst, MBM = microbasic-b-mastigophore, LG = larval gut, LE = larval epidermis. Scale bars = 100 µm.


A
BIP
MT
B
SC
MBM
C
LE
MBM
LG

a filament such as the marginal tentacle of Pachycerianthus fimbriatus due to the motion of a P. miniata larva out of a streamline is

$$N_{mf} = D/V_o d_f \qquad (1)$$

where $D = KT/3\Pi u\ dp$ (2)

(see Table 20 for definitions of symbols)

A diffusion coefficient with an external bias (Patlak, 1953; Roberts, 1975) was estimated for a planktotrophic brachiolaria (Pisaster ochraceus) by measuring the displacement amplitude of the larva away from a streamline over a period of 10 s. The diffusion coefficient has a value of $D = 6.41 + 3.59 \times 10^{-7}\ m^3\ s^{-1}$. Substitution of D into Equation 1 shows that a decrease in ambient current velocity from 0.28 to 0.01 ms^{-1} results in an increase in the time during which larval swimming takes place within the vicinity of Pachycerianthus fimbriatus tentacles, resulting in an exponential increase in the probability of contact and capture (Figure 41a). The increase in encounters with tentacles due to the swimming behavior of larvae only becomes important at velocities below 0.03 $m\ s^{-1}$. The model predicts similar results for the frequency of capture by a pore (Nmp) such as the incurrent siphon of Corella willmeriana, where

$$Nmp = (2DL)/d_c^{\,2}V_p \quad \text{(Figure 41b)} \qquad (3)$$

TABLE 20

Definitions and units of symbols used in equations 1-8.

N_{mf} = dimensionless index describing the frequency of capture by a filament or tentacle due to the swimming behavior of a brachiolaria larva

N_{mp} = dimensionless index describing the frequency of capture by a pore or siphon due to the swimming behavior of a brachiolaria larva

D = coefficient of diffusion for a brachiolaria larva (m^3 s^{-1})

B = diffusion constant for a brachiolaria larva (J K^{-1})

V_o = ambient current velocity (m s^{-1})

V_c = current velocity at the center of the incurrent siphon (m s^{-1})

V_p = current velocity at a given point across the radius of the incurrent siphon (m s^{-1})

L = length of incurrent siphon (m)

T = absolute temperature (K)

DV_t = instantaneous displacement volume of the marginal tentacles (m^3)

DV_p = instantaneous displacement volume of the incurrent paraboloid (m^3)

R = encounter radius (m) (see Gerritsen and Strickler, 1977)

R_s = radius of incurrent siphon (m)

R_p = radius at a given point across the incurrent siphon (m)

F = filtration efficiency (%)

FV = instantaneous filter volume of tentacles or incurrent paraboloid (m^3)

$\sum FV$ = total instantaneous filter volume of tentacles and incurrent paraboloids per unit area on the benthos (m^3 m^2)

M = probability of mortality during settlement (%)

W = volume of the water column immediately above the substratum (m^3)

u = dynamic viscosity of seawater (N m^{-2} s)

h = height of tentacles or incurrent paraboloid (m)

d_f = diameter of filament or tentacle (m)

d_p = diameter of brachiolaria larva (m)

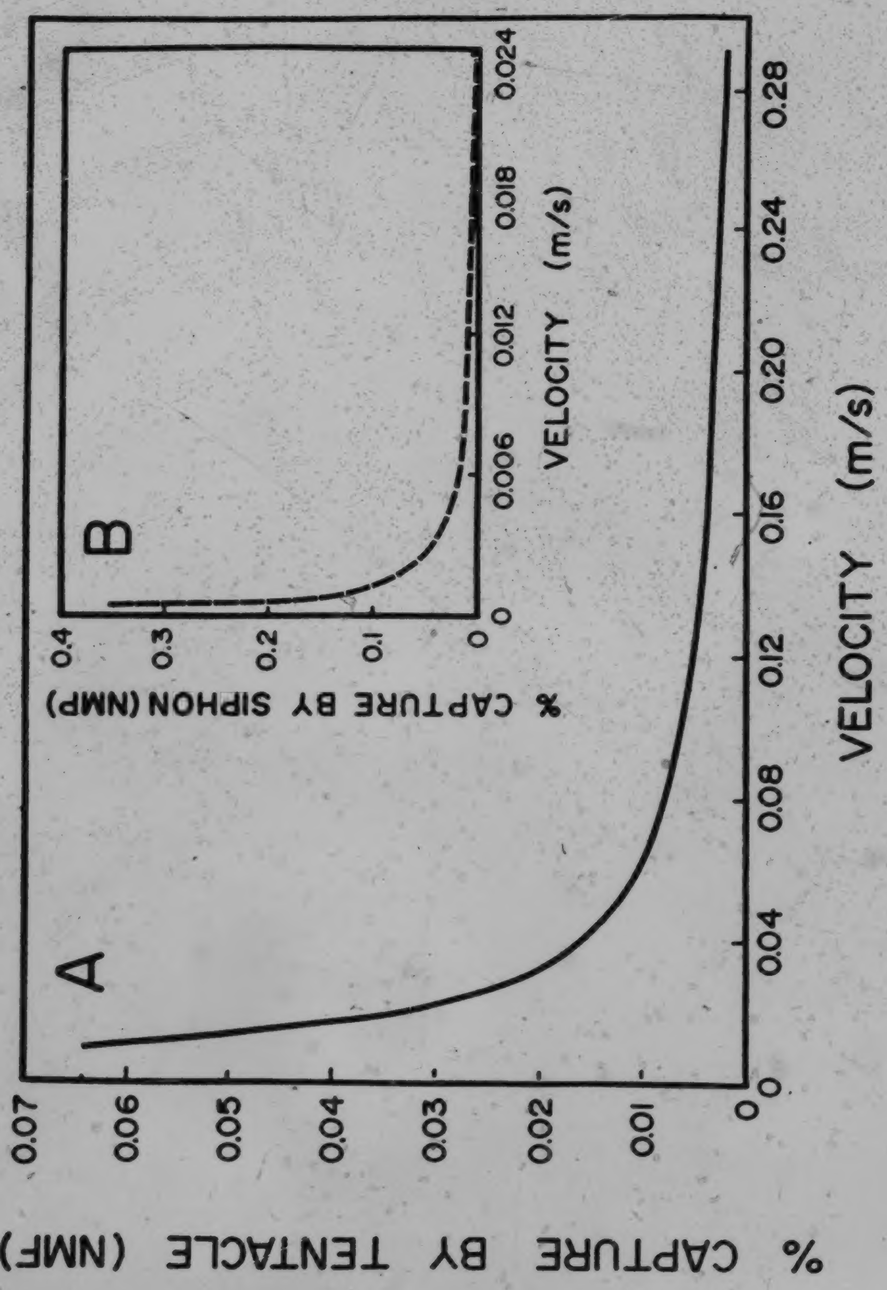
d_c = diameter of incurrent siphon (m)

r = radius of incurrent paraboloid (m)

r_1 = basal radius of tentacle or tentacle sphere (m)

r_2 = distal radius of tentacle or tentacle sphere (m)

Figure 41. Effects of current velocity on the dimensionless indicies of larval capture (N_{mf} and N_{mp}). A. Capture of *Asterina miniata* brachiolaria larvae by the marginal tentacles of *Pachycerianthus fimbriatus*. B. Capture of *A. miniata* brachiolaria larvae by the incurrent siphon of *Corella willmeriana*.


A
B
% CAPTURE BY TENTACLE (NMF)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0.04
0.08
0.12
0.16
0.20
0.24
0.28
VELOCITY (m/s)
% CAPTURE BY SIPHON (NMP)
0.4
0.3
0.2
0.1
0
0.006
0.012
0.018
0.024
VELOCITY (m/s)

and the velocity profile across the siphon is approximated by Poiseuille flow as

$$V_p = V_c[1-(R_s/R_p)^2] \qquad (4)$$

(Vogel, 1981). Velocities were adjusted by a correction factor of 30% to compensate for deviation of the incurrent siphon from a circle (see Charriaud, 1982).

The relative impact of suspension feeders on larval survival in Bamfield and Grappler Inlets was compared by estimating the probability that a settling _Asterina_ _miniata_ larva will be captured by _Pachycerianthus_ _fimbriatus_ or _Corella_ _willmeriana_. The instantaneous filter volume for a suspension feeder (FV) can be defined as the volume of water immediately above the substratum that is filtered during a specified period of feeding activity. If a settling larva enters FV it will be captured and ingested. Thus, FV is the instantaneous volume of water where the probability of mortality (M) is 100%, and is equivalent to the encounter radius (R) of Gerritsen and Strickler (1977).

Since the number of particles captured by a filter increases as a function of the fibre volume fraction (Chen, 1955; Rubenstein and Koehl, 1977), the impact of suspension feeding was gauged according to the instantaneous geometric displacement of water by the marginal tentacles of _Pachycerianthus_ _fimbriatus_, and by the instantaneous volume of water affected by the feeding activities of _Corella_ *willmeriana* (Figure 42). The instantaneous displacement volume of *P. fimbriatus* tentacles (DV_t) can be approximated by a segment of a sphere

$$DV_t = 1/6\,\Pi h(3r_1^2+3r_2^2+h^2) \qquad (5)$$

where r_1, r_2 and h are the tentacle sphere radii and height (Figure 42a). A correction factor (E) equal to the filtration efficiency of *P. fimbriatus* (0.11, see Table 19) must be applied to DV_t to compensate for spaces between the tentacles and for the ability of a *Asterina miniata* larva to escape, such that

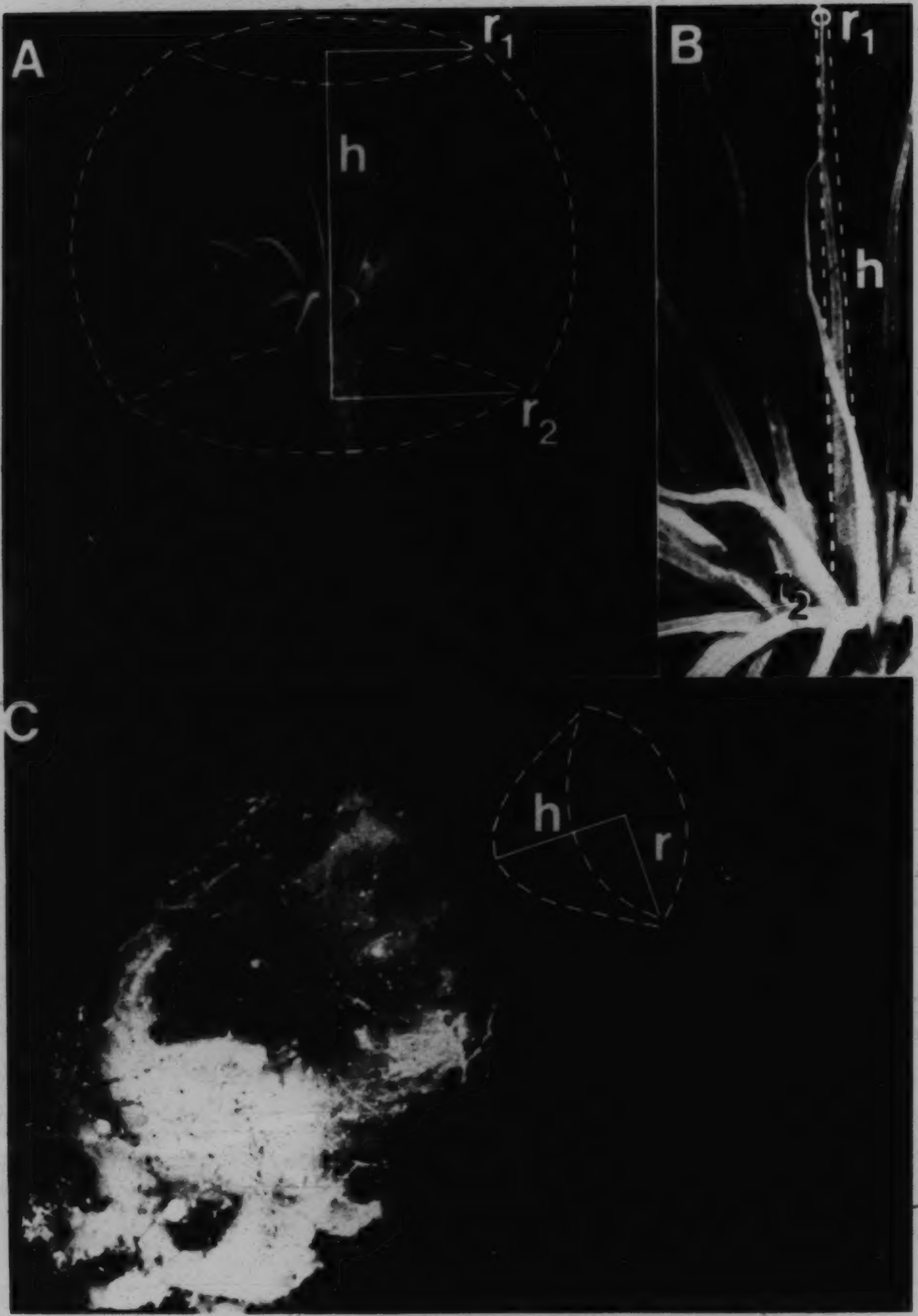
$$FV = DV_{t(sphere)}(E) \qquad (6)$$

Alternatively, the corrected instantaneous displacement volume of the marginal tentacles can be obtained directly by summing the conic displacement volumes of individual tentacles (Figure 42b) as

$$DV_{t(cone)} = 1/3\,\Pi h(r_1^2+r_1r_2+r_2^2) \qquad (7)$$

Values for FV were determined from 41 photographs of *Pachycerianthus fimbriatus* taken in the field and averaged 14.8 ± 8.4 cm^3 (sphere method) and 18.8 ± 4.0 cm^3 (cone method) per anemone. In *Corella willmeriana*, the instantaneous displacement volume of the feeding currents

Figure 42. Geometric reconstructions of the instantaneous volumes of water filtered by *Pachycerianthus fimbriatus* and *Corella willmeriana*. A. Segment of a sphere defined by the marginal tentacles of *P*. *fimbriatus*. B. Conic section defined by a marginal tentacle. C. Paraboloid defined by the feeding currents of *C*. *willmeriana*. See Table 20 for definitions of symbols.


A
r1
h
r2
B
r1
h
r2
C
h
r

(DV_p) can be approximated by a paraboloid (Figure 42c,)

$$DV_{p(\text{paraboloid})} = 1/2\,\Pi\, r^2 h \qquad (8)$$

where r and h are the radius and height above the siphon at which *Asterina miniata* larvae were captured during laboratory flow tank feeding experiments (Figure 38, Table 19). Values for DV_p range from 0.30 to 2.36 cm^3 per ascidian. The filtration efficiency of *Corella willmeriana* (E) is dependent on the developmental stage of *A. miniata* and has an average value of 0.87 for bipinnaria larvae (Table 19). The instantaneous filter volume for *C. willmeriana* (FV) is given by the product of E and $DV_{p(\text{paraboloid})}$.

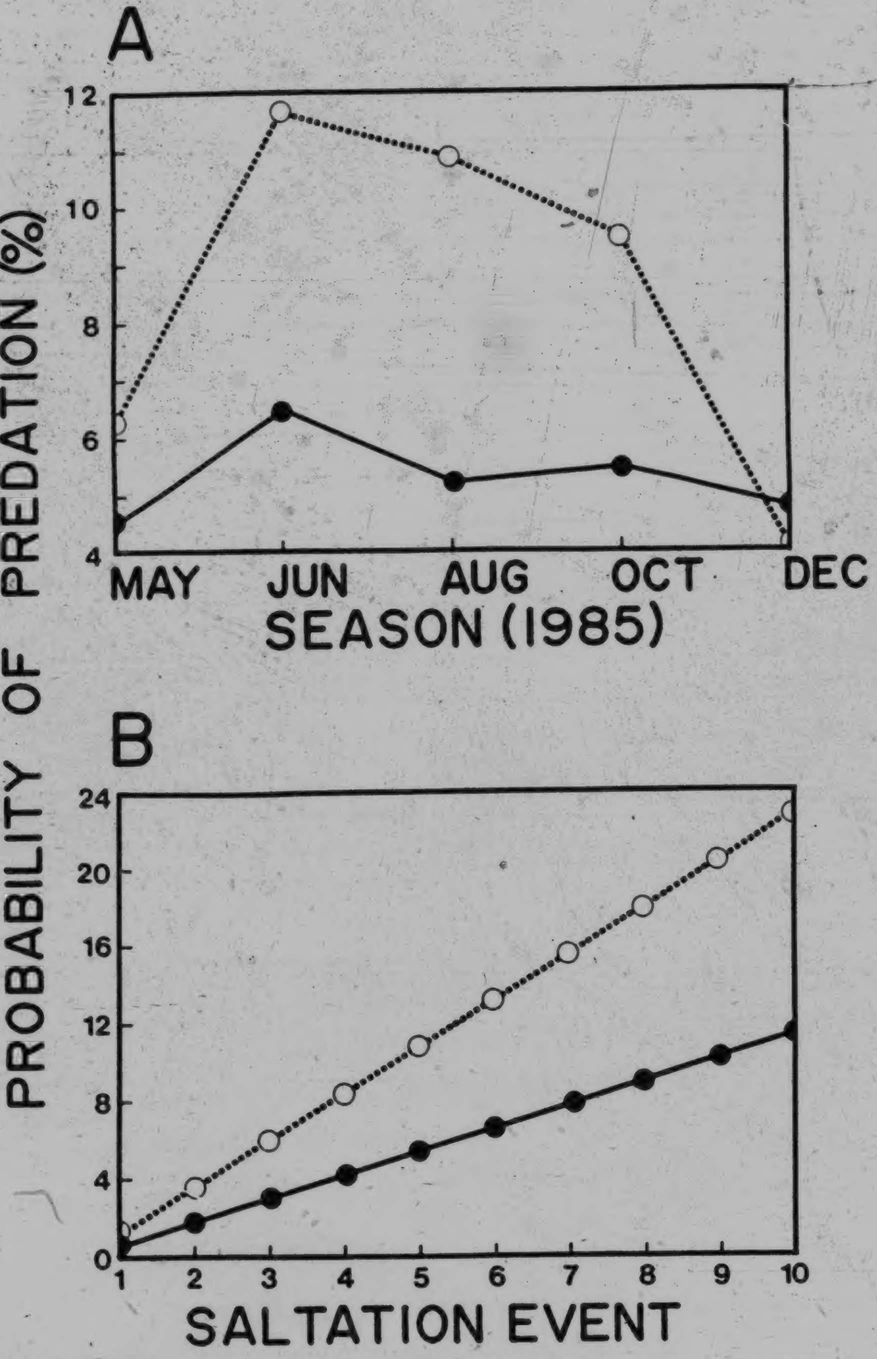
If *Corella willmeriana* and *Pachycerianthus fimbriatus* are distributed uniformly on the bottom, the instantaneous volume of water filtered per unit area ($\sum$ FV) is given by the product of FV and the densities of *C. willmeriana* and *P. fimbriatus* on the bottom of Bamfield and Grappler Inlets. Substitution of density values obtained from surveys of benthic transects (see Table 16) yields $\sum$ FV values of $3.50 \times 10^{-4}\ m^3\ m^{-2}$ for Bamfield Inlet and $1.95 \times 10^{-4}\ m^3\ m^{-2}$ for Grappler Inlet. These values indicate that the instantaneous volume of water filtered by *C. willmeriana* and *P. fimbriatus* is about 1.8 times greater in Bamfield Inlet than that filtered by suspension feeders in Grappler Inlet. Since $\sum$ FV values vary directly with seasonal changes in the density of *C. willmeriana* and *P. fimbriatus* (Figures 35 and 43a), settling *Asterina miniata* larvae are probably exposed to the greatest risk of predation by benthic suspension feeders in Bamfield Inlet as they approach the bottom during summer months when *C. willmeriana* are at their peak of abundance.

Consider that a *Asterina miniata* brachiolaria larva settles through a portion of the water column immediately above the bottom (W) having dimensions of 1m X 1m X 0.08m. The probability of larval mortality during settlement (M) varies proportionately with $\sum FV$ and nears 1 as $\sum FV$ approaches W. Substitution of empirical parameters and field measurements for $\sum FV$ yields a probability of larval mortality (M) of 1.2% during a single settlement event in Bamfield Inlet compared with 0.6% in Grappler Inlet. Since larvae of many benthic marine invertebrates, including *Asterina miniata*, repeatedly sample substrata prior to metamorphosis (Crisp, 1974; Meadows and Campbell, 1974; Rumrill, personal observations), the cumulative risk of predation by benthic suspension feeders increases relative to the number of times the larvae traverses W (Figure 43b). Results from the model (Figure 43) illustrate that encounter rates between settling *A. miniata* larvae and benthic suspension feeders are greater in Bamfield Inlet than Grappler Inlet.

7. *Juvenile Survivorship*

Two lines of evidence indicate that mortality rates of

Figure 43. Graphical model of the pooled probabilities of predation upon brachiolaria larvae of Asterina miniata during settlement by Corella willmeriana and Pachycerianthus fimbriatus. A. Seasonal differences in the probability of predation at the Bamfield Inlet (○) and Grappler Inlet (●) study sites. B. Expected effects of repeated sampling of substrata (saltation events) by a A. miniata larva on the probability of predation by both C. willmeriana and P. fimbriatus. Effects of individual predators are assumed to be additive.


A
PROBABILITY OF PREDATION (%)
12
10
8
6
4
MAY
JUN
AUG
OCT
DEC
SEASON (1985)
B
24
20
16
12
8
4
0
1
2
3
4
5
6
7
8
9
10
SALTATION EVENT

Asterina miniata may be low after juveniles reach a ray length of 0.8 cm. First, size-frequency analysis showed that juveniles of A. miniata were persistent in Grappler Inlet (Figure 30) and did not decrease in relative abundance between March 1985 and February 1986 (Table 10). Second, results from laboratory experiments indicate that juveniles of A. miniata were not susceptible to predation by several species of benthic macroinvertebrates or fish. Cancrid crabs (Cancer productus and C. magister) and juvenile ling cod (Ophiodon elongatus) did not consume any juveniles of A. miniata in feeding experiments over periods of 14 days. Juveniles of A. miniata were also not preyed upon by asteroids in experiments lasting even longer periods (Evasterias troschelli, 28 days; Dermasterias imbricata, 18 days; or Pisaster brevispinus, 31 days). Cannibalism did not occur when juveniles were confined with conspecific adults in aquaria for a period of 27 days. Only the asteroid, Pycnopodia helianthoides, preyed upon juveniles of A. miniata (Table 21).

Field caging experiments showed that losses of juvenile Asterina miniata from cages containing a male cancrid crab, Cancer productus, exceeded the loss of juveniles from a control cage. However, differences in the number of missing juveniles were not statistically significant (t = 3.46, p = 0.074). Predation upon juvenile or adult A. miniata by C. productus was never observed in natural populations during daytime SCUBA dives, and A. miniata [illegible] were

TABLE 21

Percentage of juvenile *Asterina miniata* consumed by *Pycnopodia helianthoides* in a laboratory aquarium. Table entries show mean ray lengths (± s.d.) of surviving *A. miniata*.

DAY OF EXPERIMENT	# *Asterina*	PERCENT CONSUMED	RAY LENGTH (cm)	
			Mean	(s.d.)
0	5	0	1.38	(0.15)
4	5	0	1.30	(0.07)
8	4	20	1.45	(0.13)
14	4	20	1.37	(0.15)
26	3	40	1.37	(0.15)
31	2	60	1.40	(0.14)
39	2	60	1.30	(0.14)

absent from the gut contents of 6 crabs captured near the Grappler Inlet site at night. The persistence of *A. miniata* juveniles in Grappler Inlet (Table 10), and the high survivorship in laboratory and field experiments suggest that predation upon juveniles of *A. miniata* by benthic macroinvertebrates and fish is probably not a major source of juvenile mortality.

8. *Juvenile Immigration and Emigration*

Day and Osman (1981) reported a difference in habitat use between juvenile and adult *Asterina miniata* in a subtidal boulder field in southern California. Juveniles of *A. miniata* were abundant underneath boulders while adults were found in exposed habitats. The nearest boulder field analogous to the southern California nursery area is *ca*. 3.5 km away from the study site in Grappler Inlet. Crawling rates of *A. miniata* are positively correlated with ray length (Table 22), but indicate that it would take from 3 to 6 years for *A. miniata* post-larvae and juveniles to migrate from the nearest boulder field into the Grappler Inlet site. Growth measurements show that 3-6 year old *A. miniata* are typically greater than 4 cm in ray length (Figure 31), hence the cohorts of juveniles observed in Grappler Inlet (Figure 30) most likely originated from autochthonous larval settlement within the established *A. miniata* population.

TABLE 22

Crawling speeds of *Asterina miniata* post-larvae and juveniles in the laboratory. Individuals in size class 1 were obtained following metamorphosis of brachiolariae in substratum selection experiments. Specimens in size classes 2 - 4 were collected from Grappler Inlet.

SIZE CLASS	RAY LENGTH (cm)	n	CRAWLING SPEED (cm/min) Mean	(s.d.)
1	0.06 - 0.07	8	0.09	(0.03)
2	0.24 - 0.47	14	0.26	(0.08)
3	0.71 - 1.32	6	1.80	(0.39)
4	2.42 - 2.63	9	5.61	(0.45)

KENDALL'S COEFFICIENT OF RANK CORRELATION
$W = 0.8526$ $p < 0.001$

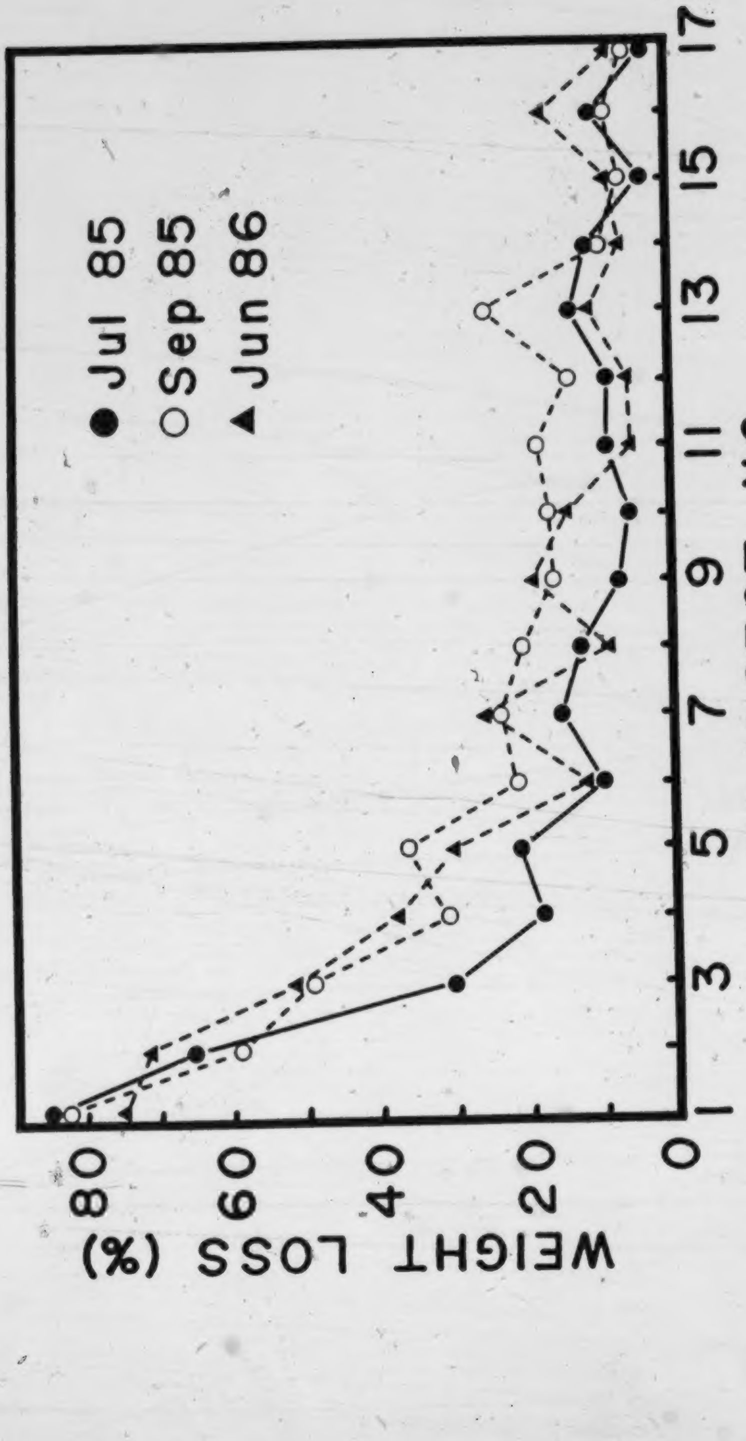
D. DISCUSSION

The spatial pattern of Asterina miniata recruitment differed markedly between two adjacent inlets in Barkley Sound. Recruits were conspicuous and abundant within an established population of A. miniata in Grappler Inlet but were absent from a population located nearby in Bamfield Inlet (Figure 30). Several alternative hypotheses can be invoked to explain the extent to which the observed pattern of A. miniata recruitment reflects processes occuring within the plankton, during settlement, and after metamorphosis. These hypotheses consider: 1) the spatial heterogeneity of larval populations, 2) substratum selection preferences of settling larvae, 3) spatial differences in the susceptibility of larvae to predation at the time of settlement, 4) differential survivorship of post-larvae and juveniles, and 5) immigration and emigration away from the initial settlement site. Collectively, these hypotheses form a framework to elucidate factors that may have contributed to the abundance of A. miniata juveniles in Grappler Inlet.

1. Reproductive Activity of Asterina miniata

The population of Asterina miniata underwent a seasonal cycle of reproductive activity in Grappler Inlet. Pyloric caecum and gonad indices exhibited low amplitude oscillations (Figure 32) that were correlated with seasonal changes in temperature and salinity (Figure 29). Cyclic

Figure 54. Exposure gradient within Barkley Sound estimated by the proportional weight loss of plaster casts along each of 17 transect lines located at various sites within Barkley Sound (see Table 26). Transects 1-5 are characterized by high exposure, 6-11 by intermediate exposure, and 12-17 by low exposure. Weight loss values indicate the mean percent loss of 3-6 casts over one complete tidal cycle. Dates indicate months when rates of weight loss were recorded.


● Jul 85
○ Sep 85
▲ Jun 86
WEIGHT LOSS (%)
0
20
40
60
80
TRANSECT NO.
1
3
5
7
9
11
13
15
17

Bamfield Inlet and 15% at Grappler Inlet. The positions of transects along the exposure gradient illustrated by the subjective ranking, sediment grain size and plaster cast indices are consistent with changes in the distribution of intertidal invertebrates and algae (Austin *et al*., 1971), and suggest that the exposure gradient shown in Figure 54 is a persistent feature among the study sites in Barkley Sound.

2. Diversity and Abundance of Barkley Sound Echinoderms

A total of 37 species of echinoderms were encountered during transect surveys at Taylor Island, Bamfield Inlet and Grappler Inlet. Counts of the cumulative number of species encountered along each transect are shown in Figures 55-57. The total number of species typically reached an asymptote after 20-24 successive quadrats in habitats occupied by less than 15 species. Asymptotes were reached after about 35 successive quadrats in habitats occupied by more than 15 species. The greatest number of species occurred along rocky bottom subtidal transects at Taylor Island and Grappler Inlet, and among wharf pilings at the Bamfield Inlet study area (Figures 55-57). Intertidal mud flats and rocky cliffs were inhabited by the lowest number of species.

Figure 58 shows the proportion of the echinoderm fauna composed of echinoids, asteroids, holothuroids, ophiuroids, and crinoids at each of 17 transects. Asteroids were found along all transect lines and composed the greatest

Figure 55. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Taylor Island study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 50).

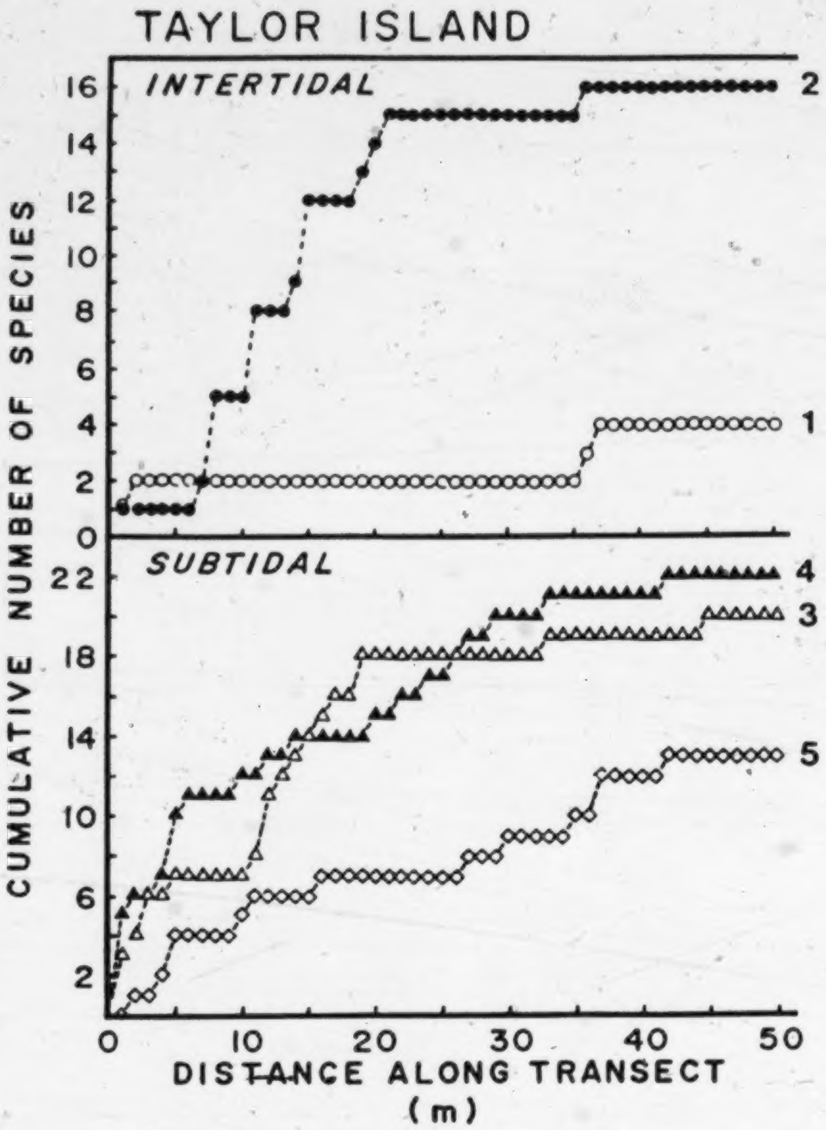

TAYLOR ISLAND
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
DISTANCE ALONG TRANSECT (m)
0
2
4
6
8
10
12
14
16
18
22
20
30
40
50
1
2
3
4
5

Figure 56. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Bamfield Inlet study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 51).

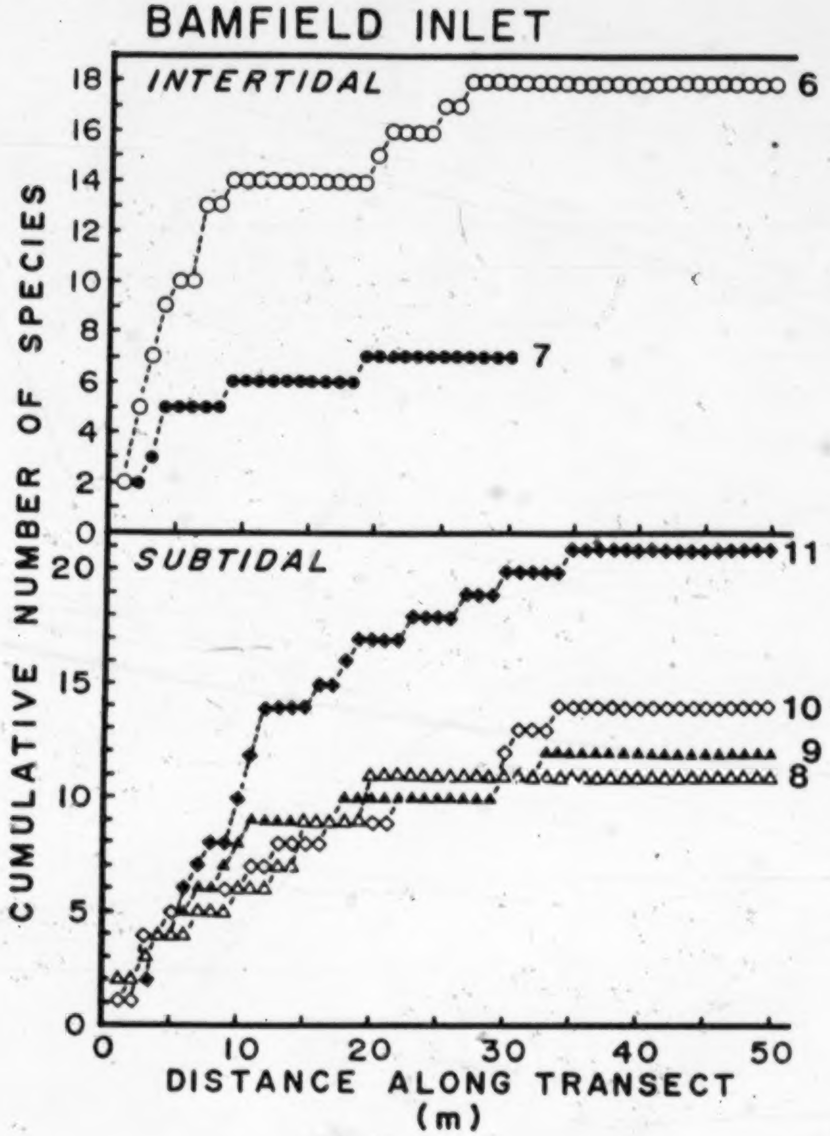

BAMFIELD INLET
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
DISTANCE ALONG TRANSECT (m)
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
0
10
20
30
40
50
6
7
11
10
9
8

Figure 57. Cumulative number of echinoderm species encountered along intertidal and subtidal transect lines at the Grappler Inlet study site. The number beside each cumulative plot indicates transect number and location (see Table 26 and Figure 51).

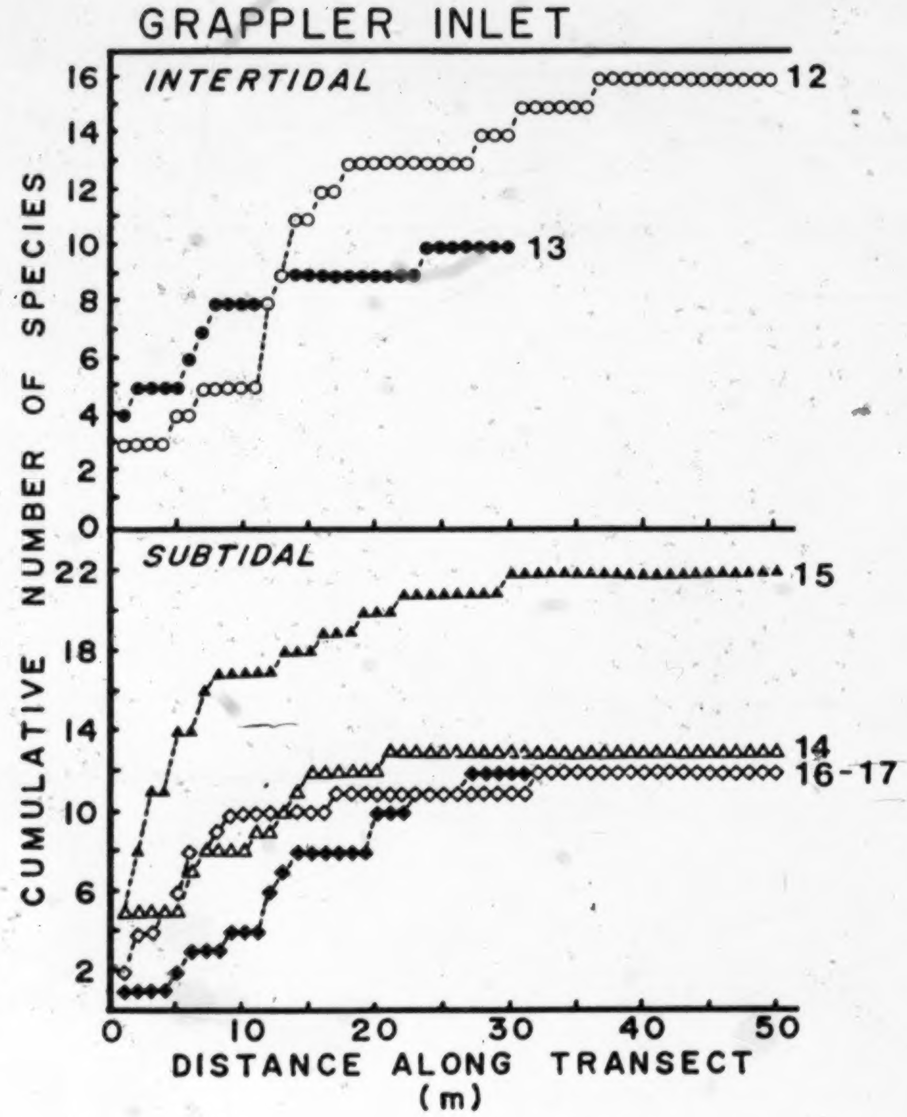
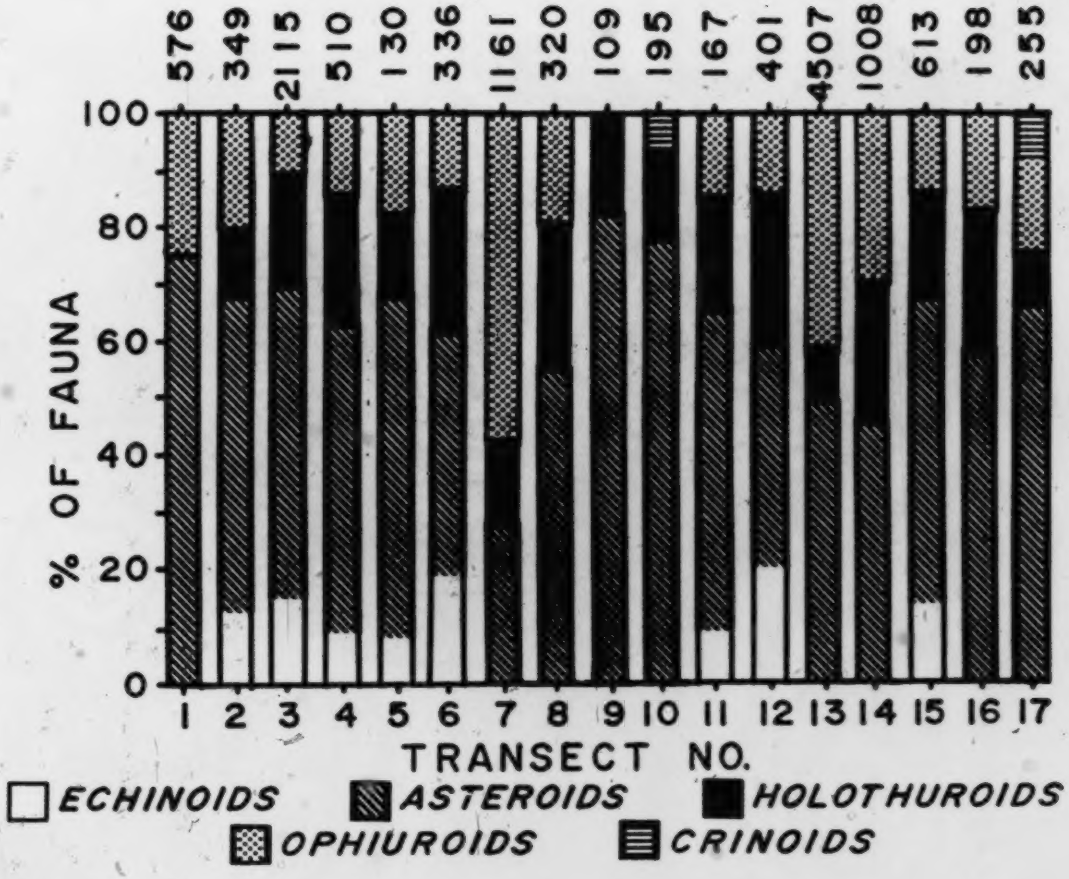

GRAPPLER INLET
INTERTIDAL
SUBTIDAL
CUMULATIVE NUMBER OF SPECIES
DISTANCE ALONG TRANSECT (m)
0
2
4
6
8
10
12
14
16
2
6
10
14
18
22
0
10
20
30
40
50
12
13
15
14
16-17

Figure 58. Proportions of the echinoderm fauna composed of echinoids, asteroids, holothuroids and crinods. Transect numbers refer to transect lines listed in Table 26. The number above each bar indicates the total number of individuals on which each proportion is based.


576
349
2115
510
130
336
1161
320
109
195
167
401
4507
1008
613
198
255
100
80
60
40
20
0
% OF FAUNA
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRANSECT NO.
ECHINOIDS
ASTEROIDS
HOLOTHUROIDS
OPHIUROIDS
CRINOIDS

proportion of the echinoderm fauna at 16 sites. Echinoids were represented at 8 sites by 3 species, and the comatulid crinoid, Florometra serratissima, occurred in deep water at two sites (Figure 58). Holothuroids were a conspicuous component of the echinoderm fauna along all transect lines except one that traversed an exposed rocky intertidal habitat. Ophiuroids were found in 15 of 17 sites (Figure 58), and they were abundant along with infaunal holothuroids in protected mud-flat habitats.

The distribution and densities of 37 species of echinoderms are listed in Tables 27 and 28. Seven species of sea urchins occur within Barkley Sound (Austin and Deutsch, 1978). However, only 3 species were encountered during quantitative sampling along benthic transects. Both the red urchin, Strongylocentrotus franciscanus, and the purple urchin, S. purpuratus, were abundant in shallow water at Taylor Island (Table 27). Densities of S. franciscanus averaged 174 ± 44 and 17 ± 6 per 10 m^2 along the 15 and 35 ft depth contours, respectively. Purple urchins averaged 19 ± 24 per 10 m^2 at 15 ft below MLLW, but their densities decreased rapidly in deeper water. The green urchin, S. droebachiensis, was common on wharf pilings and a variety of hard substrata ranging from exposed bedrock to cobble habitats in sheltered locations (Tables 27 and 28).

Although asteroids were found along all transect lines, only 2 species, Pycnopodia helianthoides and Dermasterias

TABLE 27

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters. A (+) symbol indicates species was present at the site but did not appear within a quadrat. Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ECHINOIDEA:			ASTEROIDEA:											
			SF	SP	SDR	PO	PB	PG	OK	STY	ET	LH	PH	DI	SS	SD	SPAX
Taylor Island	1.	TI.PO.E	0	0	0	107.6 50.2	0	0	0	0	0	3.8 8.5	0	0	0	0	0
	2.	TI.PO.N	0.6 0.9	18.8 23.6	+	32.0 28.7	0	0	0.4 0.5	0	0.8 1.3	5.4 4.0	0.2 0.5	0.2 0.5	0	0	0
	3.	TI.10.AB	173.7 44.9	42.0 19.3	0.8 0.8	0.4 0.5	0.1 0.3	0	1.0 1.2	0	0.1 0.3	1.2 1.1	1.4 1.3	0.4 0.7	0.1 0.3	0.6 0.9	0
	4.	TI.35.AB	17.1 5.6	0.1 0.1	0	0	0.3 0.5	0	0.8 1.0	0.3 0.5	0.2 0.4	0	0.4 0.7	0.1 0.3	0.6 0.9	0.3 0.5	0
	5.	TI.50.AB	7.0 9.4	0	0	0	0.1 0.3	0.1 0.3	0.4 0.7	0	0	0	0	0	0.1 0.3	1.0 1.4	0

TABLE 27 (continued)

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ASTEROIDEA: SE	LOF	CP	HL	HNS	HA	PT	MA	PM	LF	HOLOTHUROIDEA: PC	CM	CPIP	EO	PSOL	LC
Taylor Island																		
	1.	TI.PO.E	0	0	0	0	0.6 1.3	0	0	0	0	0	0	0	0	0	0	0
	2.	TI.PO.N	0	0	0	0.2 0.5	0.4 0.9	0	0	0	0.4 0.5	0	0	3.2 5.1	0	0.6 1.3	0	0
	3.	TI.10.AB	0	0	0	1.4 1.8	0.2 0.4	0	0	PB 0	0	0	2.1 4.0	1.9 2.3	0.2 0.4	0.6 0.9	+	0
	4.	TI.35.AB	0	0	0	5.4 3.0	0.2 0.4	0	0.2 0.4	0.2 0.4	0	0	1.8 1.1	13.7 22.8	1.6 1.5	0.8 1.1	3.9 3.9	0
	5.	TI.50.AB	0	0	0.3 0.7	0.2 0.4	0.1 0.1	0	0	0	0	0	1.4 1.2	+	+	0.1 0.3	0	0

TABLE 27 (continued)

Population densities of echinoderms along 5 transect lines at Taylor Island. Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	OPHIUROIDEA: OA	AO	AU	AP	CRINOIDEA: AX	FS	INDEX OF DIVERSITY: TOTAL # Spp.	SHANNON Hn	SIMPSON Dn	COMMUNITY α	VARIETY V
Taylor Island	1.	TI.PO.E	0	0	0	0	3.4 1.7	0	4	0.30	0.13	0.58	1.09
	2.	TI.PO.N	1.0 1.7	0.2 0.5	0	0	5.4 2.9	0	16	1.60	0.72	3.46	5.89
	3.	TI.10.AB	35.8 37.5	+	0	0	113.7 68.3	0	20	0.66	0.31	3.06	5.71
	4.	TI.35.AB	10.2 6.0	3.5 3.7	0	0	6.2 6.7	0	22	1.77	0.75	4.68	7.76
	5.	TI.50.AB	+	5.8 4.0	0	0	7.1 6.2	0	13	1.17	0.50	3.60	5.68

TABLE 28

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets. Table entries show the mean and s.d. (below) number of individuals per 10 square meters. A (+) symbol indicates species was present at the site but did not appear within a quadrat. Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ECHINOIDEA: SF	SP	SDR	ASTEROIDEA: PO	PB	PG	OK	STY	ET	LH	PH	DI	SS	SD	SPAX
Bamfield Inlet	6.	BI.COB.AB	0.6 0.9	7.8 6.2	1.4 1.5	16.6 6.2	0	0	0.6 0.9	0	0	27.4 13.6	+	0.8 0.8	0	0.2 0.4	0
	7.	BI.MUD.AB	0	0	0	0	+	0	0	0	0.4 1.3	0	0	0.4 0.9	0	0	0
	8.	BI.15.AB	0	0	0	0	0.4 0.5	0	0	0	0.4 0.5	0	0.4 0.7	0.5 0.7	0	0	0
	9.	BI.40.AB	0	0	0	0	3.0 2.3	0	1.0 0.7	0	1.5 1.3	0	1.8 1.5	0.6 0.5	0.2 0.4	0.1 0.3	0
	10.	BI.85.AB	0	0	+	0	0.2 0.6	0	1.0 0.3	0	+	0	0.1 0.3	0	0.4 0.7	0.6 0.8	0
	11.	BI.PILE.AB	0.3 0.7	0	0.1 0.3	+	0.5 0.7	0	0.7 0.8	0	0.9 1.0	+	2.7 2.2	1.8 1.2	0.6 0.8	0.2 0.4	0.1 0.3
Grappler Inlet	12.	GI.COB.AB	0.6 0.9	18.4 15.1	2.6 1.8	4.2 4.6	0	0	0.2 0.4	0	0	10.4 6.2	0	1.0 0.7	0	0	0
	13.	GI.MUD.AB	0	0	0	0.5 1.1	+	0	0	0	0	0.7 2.1	0.4 0.9	0.4 0.9	0	0	0
	14.	GI.20.AB	0	0	0	0.6 0.7	1.2 0.4	0	+	0	0.9 1.0	0	1.6 1.3	1.6 1.3	0	0	0
	15.	GI.35.AB	0.8 1.0	0.3 0.5	2.4 2.5	0	0.4 0.5	0	+	0	0.2 0.4	0	2.1 1.4	1.1 1.0	0.3 0.5	0.2 0.4	0
	16.	GI.40.AB	0	0	0	0	1.3 0.9	0	0.1 0.3	0	0.2 0.4	0	1.3 1.2	0.5 0.5	0.5 0.7	0	0
	17.	GI.60.AB	0	0	0	0	0.3 0.5	0	0	0	0.7 1.1	0	0.4 0.5	0	0.2 0.4	0.2 0.6	0

TABLE 28 (continued)

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets.
Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE	#	TRANSECT CODE	ASTEROIDEA: SE	LOF	CP	HL	HNS	HA	PT	MA	PM	LF	HOLOTHUROIDEA: PC	CM	CPIP	ED	PSOL	LC
Bamfield Inlet	6.	BI.COB.AB	0	0	0	1.0 1.0	0.6 0.9	0	0	0	0	0	0.2 0.4	2.1 1.2	0.4 0.6	1.0 1.4	+	0
	7.	BI.MUD.AB	0	0	0	0	0	0	0	0	+	0	+	0	0	0	0	132.2 68.1
	8.	BI.15.AB	0	0	0	+	0	0	0	+	14.1 3.6	0	0.2 0.4	0.9 1.7	+	0	0	4.3 8.6
	9.	BI.40.AB	0.1 0.3	0	0	0.6 0.7	0	0	0	0	0	0	1.3 1.2	0.1 0.3	+	0	0	0
	10.	BI.85.AB	+	0.2 0.6	1.4 1.2	0.8 1.0	0	0	0.2 0.4	11.2 5.1	0	0.1 0.3	1.4 1.3	0	0.3 0.5	0	0	0
	11.	BI.PILE.AB	0	0	0.2 0.6	2.2 1.7	0	0.1 0.3	0	1.2 1.4	0	0	1.2 1.0	1.6 1.7	0.4 0.7	0.5 0.7	+	0
Grappler Inlet	12.	GI.COB.AB	0	0	0	0.8 1.3	16.6 16.9	0	0	+	0	0	0	8.6 6.8	0.4 0.6	1.0 1.0	0.6 1.3	0
	13.	GI.MUD.AB	0	0	0	0	0	0	0	0	0.8 2.1	0	+	0	0	0	0	407.3 229.6
	14.	GI.20.AB	0	0	0	0	0	0	0	0	61.3 21.5	0	1.1 1.1	1.7 6.1	0	0	0	632.3 956.4
	15.	GI.35.AB	0.1 0.3	0	0.7 0.7	7.0 3.6	5.9 3.8	0	0.1 0.3	2.2 2.4	0	0	2.3 1.9	11.1 2.6	1.4 1.4	0	2.6 2.7	0
	16.	GI.40.AB	0	0	0	0	0	0	0	0	4.3 1.6	0	1.7 0.9	0.9 1.9	0.2 0.4	0	0	0
	17.	GI.60.AB	0	+	1.5 1.1	0.6 0.7	0	0	0	15.2 7.8	0	+	0.6 0.7	0	0	0	0	0

TABLE 28 (continued)

Population densities of echinoderms along 12 transect lines in Bamfield and Grappler Inlets.
Table entries show the mean and s.d. (below) number of individuals per 10 square meters.
A (+) symbol indicates species was present at the site but did not appear within a quadrat.
Genus and species names are abbreviated (see Table 30).

STUDY SITE			OPHIUROIDEA:					CRINOIDEA:		INDEX OF DIVERSITY			
	#	TRANSECT CODE	OA	AO	AU	AP	AX	FS	TOTAL # Spp.	SHANNON Hn	SIMPSON Dn	COMMUNITY α	VARIETY V
Bamfield Inlet													
	6.	BI.COB.AB	1.4 1.5	4.7 3.9	0.1 0.2	+	5.2 5.4	0	18	1.79	0.75	4.07	6.73
	7.	BI.MUD.AB	0	14.3 12.7	5.1 3.8	0.9 1.2	1.3 4.7	0	7	0.42	0.21	0.99	1.96
	8.	BI.15.AB	0	14.4 7.2	0.1 0.4	0	0.7 1.3	0	11	1.17	0.60	2.21	3.99
	9.	BI.40.AB	0	0.4 0.6	+	0	0	0	12	1.98	0.83	3.44	5.40
	10.	BI.85.AB	0	0	0	0	0	0.3 0.5	14	1.42	0.56	3.46	5.68
	11.	BI.PILE.AB	1.1 1.0	0.1 0.3	0	0	0.2 0.4	0	21	2.65	0.91	6.35	9.00
Grappler Inlet													
	12.	GI.COB.AB	4.4 4.6	16.8 7.4	0	0	10.4 8.3	0	16	2.13	0.85	3.33	5.76
	13.	GI.MUD.AB	0	157.2 122.3	1.3 4.2	6.3 14.2	16.7 17.6	0	10	0.79	0.45	1.22	2.46
	14.	GI.20.AB	0	1216 708	2.0 4.4	40.5 128.2	445.9 403.1	0	13	1.36	0.59	2.11	3.99
	15.	GI.35.AB	12.8 13.4	405.3 573.2	+	0	851.2 905.4	0	22	2.47	0.89	4.46	7.53
	16.	GI.40.AB	0	3.6 1.9	+	+	108.8 213.7	0	12	1.92	0.79	2.81	4.79
	17.	GI.60.AB	0	202.7 393.9	+	+	486.4 912.4	0.2 0.4	12	1.44	0.60	2.61	4.57

imbricata, occurred at 12 or more sites. The common species of asteroids occurred at 5 - 11 sites (mean = 8, s.d. = 2), and rare species were encountered at 1 or 2 sites (Tables 27 and 28). The density of Pisaster ochraceus exceeded 10 m^{-2} along rocky intertidal habitats at Taylor Island and averaged about 2 m^{-2} along a cobble transect in Bamfield Inlet. Two species of forcipulate asteroids, Leptasterias hexactis and P. ochraceus made up 12 to 50% of the total echinoderm fauna at three of the intertidal sites (1:TI.POE, 2:TI.PON, 6:BI.COB). Predatory asteroids were represented by 9 to 11 species along muddy bottom habitats at depths greater than 40 ft in Bamfield Inlet where Pisaster brevispinus, Orthasterias koehleri, Evasterias troschelli, and Pycnopodia helianthoides occurred at densities from 1 to 3 per $10m^2$. The valvatid species, Mediaster aequalis, and the circumboreal spinulosid species, Crossaster papposus, were both common on shell rubble and worm tubes of Phyllochaetopterus prolifera in deep water. Other asteroids found occasionally in deep water included Solaster paxillatus and Lophaster furcilliger. Six species of asteroids were found at a single site (Tables 27 and 28). One of these, Pisaster giganteus, is at the northern extreme of its geographic range in Barkley Sound, and is infrequently reported north of Cape Flattery, Washington (Feder, 1980).

The greatest diversity of ophiuroids (4 species) occurred along transect lines that sampled mudflats and shallow subtidal habitats within Bamfield and Grappler Inlets. Densities of the amphiurid ophiuroids, *Amphiodia* (*Diamphiodia*) *occidentalis*, *A*. *urtica*, *A*. *periercta*, and *Amphipholis* (*Axiognathus*) *squamata* were greater within mudflats and shallow soft-substratum habitats in Grappler Inlet than within similar habitats in Bamfield Inlet (Tables 27 and 28). Individuals of *A*. *occidentalis* were also abundant at the 35 and 50 ft depth contours at Taylor Island. Two species of ophiuroids (*A*. *occidentalis* and *A*. *squamata*) occurred along 16 out of 17 transects. The absence of *A*. *squamata* from 40 and 85 foot depths in Bamfield Inlet was unexpected because this species was abundant at similar depths in Grappler Inlet and at Taylor Island (Tables 27 and 28).

Holothuroids occurred in nearly equal abundance and diversity along three transect lines. These included the subtidal rock wall and boulder field habitat at Taylor Island, and the cobble and wharf piling habitats at Bamfield Inlet (Tables 27 and 28). The diversity of holothuroids was also similar within the cobble habitat in Grappler Inlet. The deposit feeding aspidochirote holothuroid, *Parastichopus* *californicus*, was common in subtidal habitats at depths greater than 12 ft below MLLW.

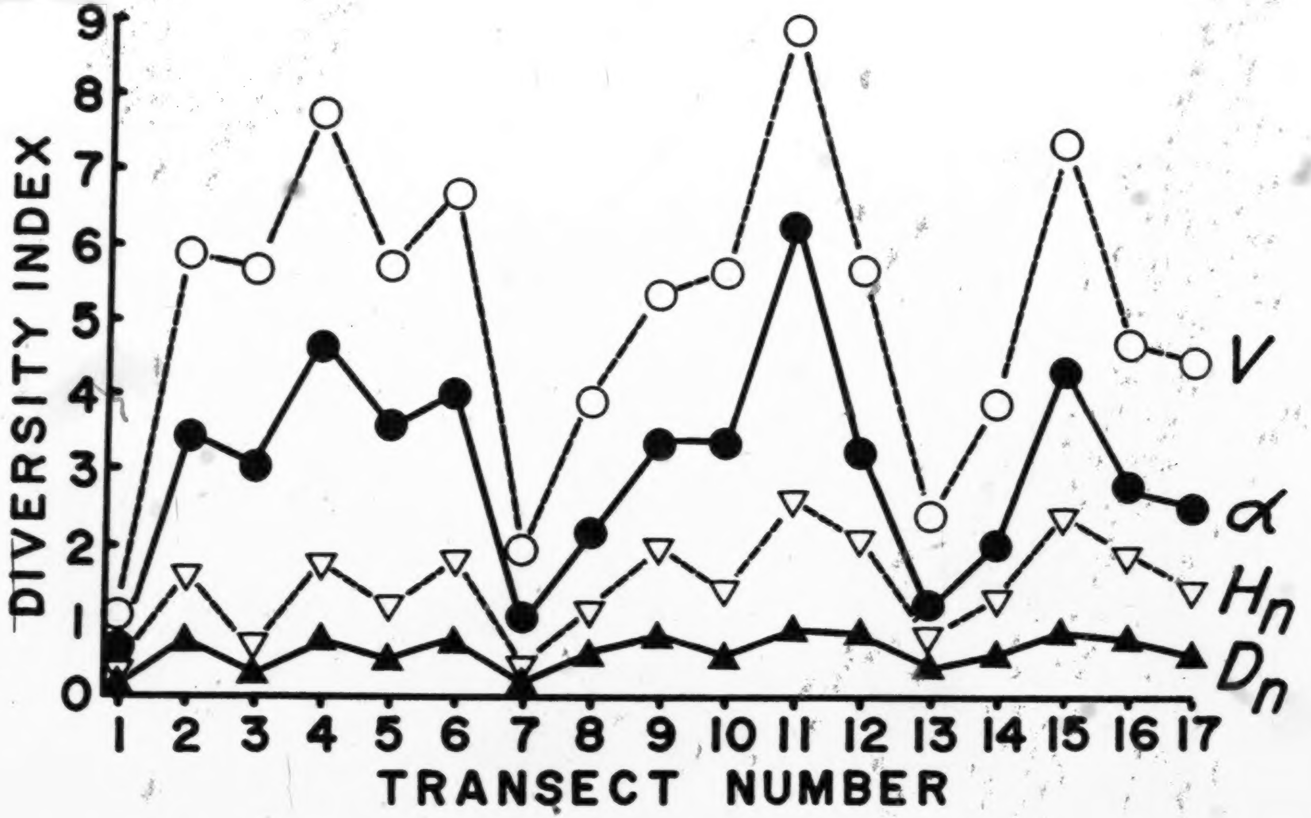
Low numbers of the comatulid crinoid, *Florometra* *serratissima*, occurred in deep water near the confluence of Bamfield and Grappler Inlets (Tables 27 and 28). These populations of *F*. *serratissima* were probably established during 1960 - 1970 by the release of dredged specimens. The typical habitat of F. serratissima is along deep water hard substratum pinnacles and rock walls swept by persistent currents.

Differences in species composition and abundance were striking between Bamfield and Grappler Inlets despite their close proximity and similar types of habitats (Tables 27 and 28). Five species of ophiuroids and the infaunal holothuroid, Leptosynapta clarki, were generally more abundant in Grappler Inlet than Bamfield Inlet. Only Amphiodia urtica occurred in greater densities in Bamfield Inlet (7:BI.MUD.AB) compared to a similar habitat in Grappler Inlet (13:GI.MUD.AB). Predatory asteroids were abundant in Grappler Inlet along transects that sampled intertidal mudflats and subtidal soft substratum habitats. In contrast, the densities of echinoids and asteroids were similar along intertidal cobble transects within Bamfield and Grappler Inlets.

Three sites were exceptional in the number of species encountered during quantitative sampling of the transects. The boulder field habitats located at Taylor Island and Grappler Inlet were each inhabited by 22 species of echinoderms. A third site among wharf pilings (11:BI.PILE.AB) was occupied by 21 species (Tables 27 and 28).

Figure 59 summarizes the diversity index values obtained for each of the 17 transect lines. All 4 indices

Figure 59. Comparison of four measures of echinoderm faunal diversity along 17 transect lines. V = index of faunal variety, α = index of community diversity, H_n = Shannon-Wiener index of diversity, D_n = Simpson's index of diversity. Equations for the various diversity indices are provided in the text. Transect numbers refer to transects listed in Table 26.


9
8
7
6
5
4
3
2
1
0
DIVERSITY INDEX
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
TRANSECT NUMBER
V
α
H_n
D_n

gave low rankings to the intertidal rock wall at Taylor Island (1:TI.PO.E) and the intertidal mudflats in Bamfield and Grappler Inlets (7:BI.MUD.AB and 13:GI.MUD.AB). High diversity index values were obtained for the transect that sampled subtidal wharf pilings in Bamfield Inlet (11.BI.PILE.AB) and for the subtidal boulder field in Grappler Inlet (15:GI.35.AB). High diversity ranks were also given to the intertidal (2:TI.PO.N) and subtidal (4:TI.35.AB) boulder field habitats at Taylor Island. The results from these diversity indices are similar to ranks based on species richness (Tables 27 and 28), and all of the measures showed similar patterns of diversity in their assessment of the transect lines.

The value of diversity indices depend upon their capacity to provide reliable and meaningful comparative descriptions within particular habitats. With the exception of 2 sites (8:BI.15.AB and 14:GI.20.AB), quantitative surveys of the transect lines were completed on a single occasion. Sampling heterogeneous echinoderm assemblages at a single point in time provides a snapshot view of the communities. Consequently, it is not possible to evaluate the variance associated with the diversity index values shown in Figure 59. Two measures were used in later evaluations of community patterns obtained from the static sample. Both Simpson's Index (D_n), and the Shannon-Wiener Index (H_n) were used to analyze relationships between life history traits and community composition because they are sensitive to the distribution of individuals among faunal assemblages (Levins 1966; Loya, 1971; Krebs, 1978).

3. Echinoderm Life History Traits

Ova sizes and modes of development differ among members of the Barkley Sound echinoderm fauna (Table 29); 17 species have planktotrophic development (47%), 15 species have lecithotrophic development (42%), and 4 species brood their offspring (11%). The distribution of ova diameters is bimodal (Figure 60). Species with planktotrophic development have ova ranging from 85 to 200 µm in diameter. Small ova from the viviparous hermaphroditic ophiuroid, *Amphipholis squamata*, occur in the first mode along with planktotrophic species in Figure 60. Ova from the remaining species range from 200 to 1300 µm in diameter. This group includes 16 lecithotrophic species and 3 brooding species (Table 29, Figure 60). The planktotrophic and lecithotrophic species are gonochoric and free-spawning with external fertilization and development. Most of the brooding species are also gonochoric, and either brood benthic external egg masses (*Leptasterias hexactis* and *Henricia* sp. nov.) or incubate their offspring internally within the coelom (*Leptosynapta clarki*).

The breeding seasons of 32 species of echinoderms are shown in Table 30. The majority of species breed during the spring and early summer months from March to June. Three species, *Amphiodia occidentalis*, *Leptasterias hexactis*, and *Leptosynapta clarki* breed primarily during winter. The

TABLE 29

Comparison of larval trophic modes, larval types, ova diameters, and maximum fecundities of echinoderms from Barkley Sound.

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter (µm)		Fecundity Max. # Ova per Female
		n	mean ± (s.d.)	
Echinoidea:				
Strongylocentrotus franciscanus	P: echinopluteus	100	152 ± (4)	2.9 X 10^7
Strongylocentrotus purpuratus	P: echinopluteus	100	85 ± (5)	1.7 X 10^7
Strongylocentrotus droebachiensis	P: echinopluteus	100	156 ± (4)	3.8 X 10^5
Holothuroidea:				
Parastichopus californicus	P: auricularia doliolaria	50	189 ± (9)	2.6 X 10^6
Cucumaria miniata	L: doliolaria	24	525 ± (9)	1.6 X 10^5
Cucumaria piperata •	L: doliolaria	21	540 ± (10)	9.2 X 10^3
Eupentacta quinquesimita •	L: doliolaria	18	392 ± (16)	3.8 X 10^4
Psolus chitonoides	L: doliolaria	34	630 ± (7)	1.5 X 10^4
Leptosynapta clarki •	B: vitellaria pentacula	22	302 ± (17)	1.2 X 10^3
Ophiuroidea:				
Ophiopholis aculeata	P: ophiopluteus	50	115 ± (6)	2.5 X 10^5
Amphiodia occidentalis	P: ophiopluteus	50	103 ± (5)	7.8 X 10^4
Amphiodia urtica •	P: ophiopluteus ?	26	101 ± (8)	
Amphiodia periercta •	P: ophiopluteus ?	32	96 ± (6)	
Amphipholis squamata •	B: vestigial ophiopluteus	9	98 ± (6)	11

TABLE 29 (continued)

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter (µm)		Fecundity
		n	mean ± (s.d.)	Max. # Ova per Female
Asteroidea:				
Pisaster ochraceus	P: bipinnaria brachiolaria	100	160 ± (6)	5.6 X 10^6
Pisaster brevispinus	P: bipinnaria brachiolaria	32	156 ± (4)	9.3 X 10^5
Orthasterias koehleri	P: bipinnaria brachiolaria	100	139 ± (5)	9.4 X 10^5
Stylasterias forreri *	P: bipinnaria brachiolaria	28	152 ± (5)	
Evasterias troschelli	P: bipinnaria brachiolaria	47	144 ± (3)	2.4 X 10^7
Leptasterias hexactis	B: modified brachiolaria	49	986 ± (21)	921
Pycnopodia helianthoides	P: bipinnaria brachiolaria	40	134 ± (4)	12.7 X 10^7
Dermasterias imbricata	P: bipinnaria brachiolaria	100	172 ± (7)	1.3 X 10^7
Solaster stimpsoni	L: modified brachiolaria	36	922 ± (21)	7.2 X 10^4
Solaster dawsoni	L: modified brachiolaria	29	962 ± (13)	3.1 X 10^4
Solaster paxillatus *	L: modified brachiolaria	18	900 ± (41)	
Solaster endeca *	L: modified brachiolaria	14	1112 ± (37)	
Lophaster furcilliger *	L: modified brachiolaria ?	12	354 ± (16)	
Crossaster papposus	L: modified brachiolaria	25	820 ± (8)	427
Henricia leviuscula	L: modified brachiolaria	25	605 ± (13)	

TABLE 29 (continued)

Class: Genus species	Larval Trophic Mode & Type P / L / B	Ova Diameter (µm)			Fecundity Max. # Ova per Female
		n	mean ±	(s.d.)	
Henricia sp. nov.	B: modified brachiolaria	25	891 ±	(12)	
Henricia asthenactis *	L: modified brachiolaria ?	17	865 ±	(15)	
Pteraster tesselatus	L: modified brachiolaria	12	1327 ±	(30)	2.7 X 10^3
Mediaster aequalis	L: modified brachiolaria	37	1049 ±	(68)	1.4 X 10^3
Patiria miniata	P: bipinnaria brachiolaria	100	137 ±	(6)	4.4 X 10^5
Luidia foliolata *	P: bipinnaria	45	154 ±	(4)	
Crinoidea:					
Florometra serratissima	L: doliolaria	39	216 ±	(8)	1.1 X 10^4

Most ova measured from natual spawnings that occurred in laboratory aquaria. Asterisk (*) indicates ova measured from excised gravid ovaries. P = planktotrophic, L = lecithotrophic, B = brooding. Question mark indicates species where larval trophic mode and type are inferred from ova diameter.

Figure 60. Distribution of ova diameters among 36 species of echinoderms listed in Table 29. The distribution is best fit by a log-normal curve (chi^2 = 14.11, $p < 0.001$); ln transformed data are strongly bimodal.

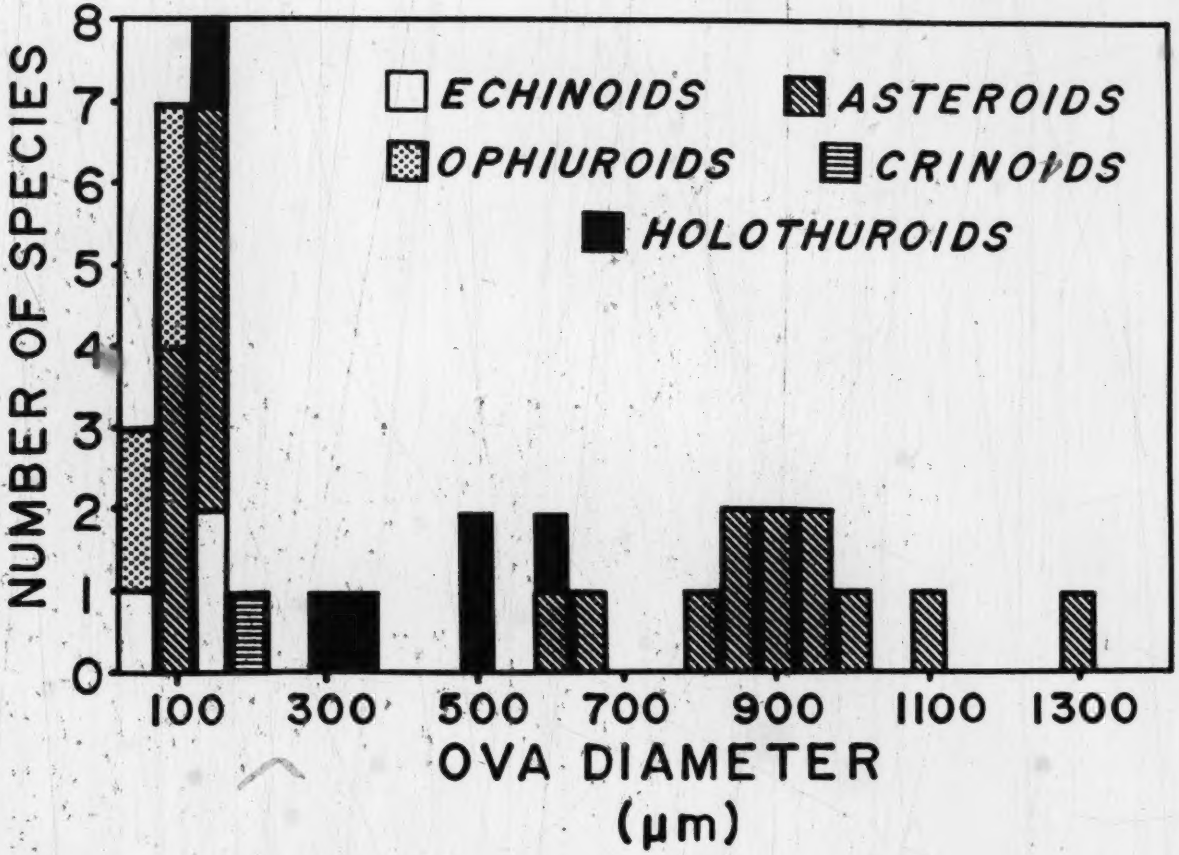
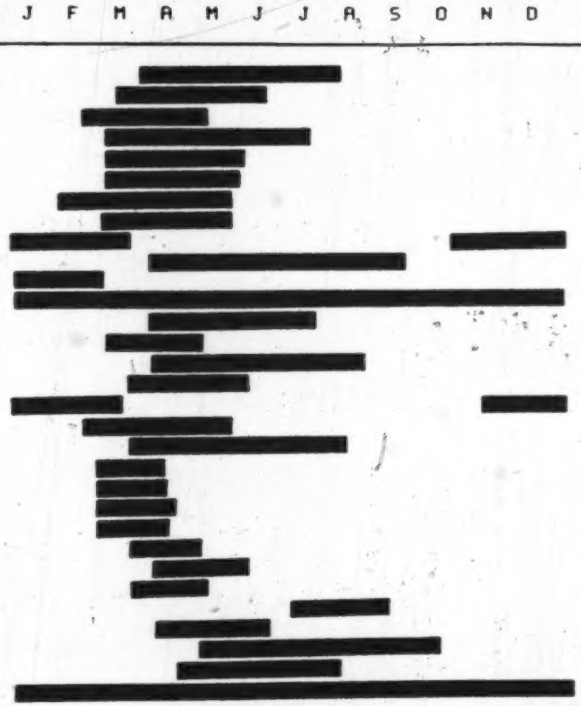

NUMBER OF SPECIES
0
1
2
3
4
5
6
7
8
100
300
500
700
900
1100
1300
OVA DIAMETER
(μm)
ECHINOIDS
ASTEROIDS
OPHIUROIDS
CRINOIDS
HOLOTHUROIDS

TABLE 30

Breeding seasons of echinoderms from Barkley Sound.
Code column indicates species abbreviations used elsewhere in the text.

CODE	Genus and species	REFERENCE
SF	Strongylocentrotus franciscanus	Bennett and Giese, 1955
SP	Strongylocentrotus purpuratus	Cochran and Englemann, 1975
SDR	Strongylocentrotus droebachiensis	Himmelman, 1978
PC	Parastichopus californicus	McEuen, 1986
CM	Cucumaria miniata	personal observations
CPIP	Cucumaria piperata	McEuen, 1986
EQ	Eupentacta quinquesimita	McEuen, 1986
PSOL	Psolus chitonoides	McEuen, 1986
LC	Leptosynapta clarki	McEuen, 1986
OA	Ophiopholis aculeata	personal observations
AO	Amphiodia occidentalis	Rumrill and Pearse, 1985
AX	Amphipholis squamata	Rumrill and Pearse, 1985
PO	Pisaster ochraceus	Mauzey, 1966
PB	Pisaster brevispinus	personal observations
OK	Orthasterias koehleri	personal observations
ET	Evasterias troschelli	Strathmann (in press)
LH	Leptasterias hexactis	Chia, 1966a
PH	Pycnopodia helianthoides	Greer, 1962
DI	Dermasterias imbricata	personal observations
SS	Solaster stimpsoni	S. Carson, pers. comm.
SD	Solaster dawsoni	S. Carson, pers. comm.
SPAX	Solaster paxillatus	S. Carson, pers. comm.
SE	Solaster endeca	S. Carson, pers. comm.
CP	Crossaster papposus	Strathmann (in press)
HL	Henricia leviuscula	Strathmann (in press)
HNS	Henricia nov. sp.	personal observations
PT	Pteraster tesselatus	Chia, 1966b
MA	Mediaster aequalis	Lambert, 1981
PM	Patiria miniata	Rumrill, 1987
LF	Luidia foliolata	Lambert, 1981
FS	Florometra serratissima	Mladenov, 1980



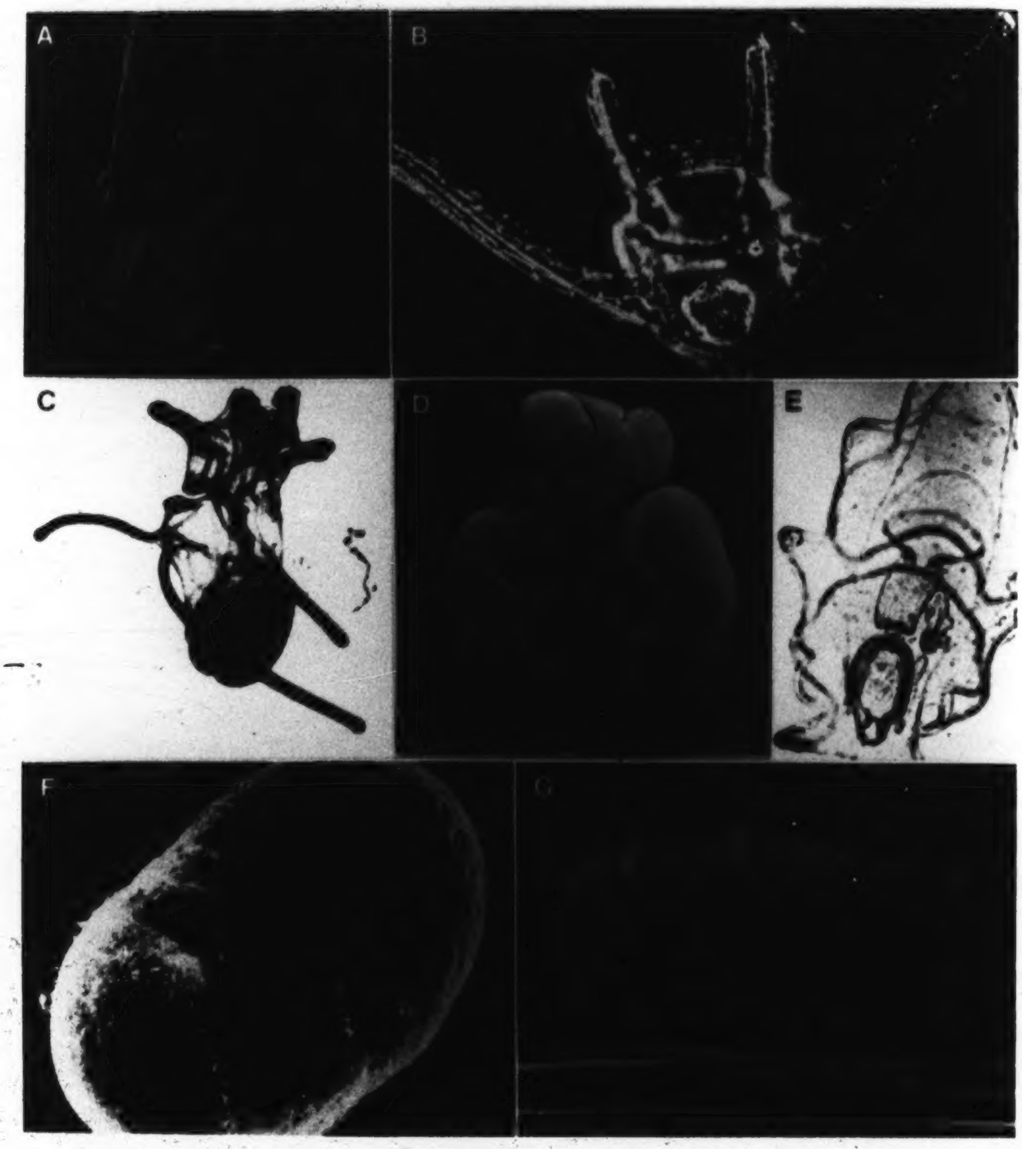
* Abbreviation codes for other species listed in Tables 27 and 28 include: PG = Pisaster giganteus, STY = Stylasterias forreri, LOF = Lofaster furcilliger, HA = Henricia asthenactis, AU = Amphiodia urtica, AP = Amphiodia periercta.

species with lecithotrophic development generally have short breeding seasons and reproduce early in the spring. In contrast, species with planktotrophic development have longer (3-5 month) breeding periods. Two species, *Amphipholis squamata* and *Florometra serratissima*, reproduce throughout the year (Table 30).

Morphological characteristics of the various types of echinoderm larvae are illustrated in Figure 61. All types of echinoderm larvae swim with cilia. In the planktotrophic echinopluteus, ophiopluteus, auricularia and brachiolaria larvae the cilia are concentrated along an elaborate looping band. In contrast, the cilia of lecithotrophic holothuroid and crinoid larvae are organized into rings that encircle the larval body. Finally, in the modified brachiolaria of lecithotrophic asteroids the cilia are scattered throughout the larval epidermis. Maximum body lengths of the metamorphically competent larval stages approach 1 mm in the planktotrophic species and range from 1 to 2 mm in the lecithotrophic species.

Estimates of the maximum number of ova per female are shown for 26 species in Table 29. These estimates underestimate the number of ova spawned during an extended period of reproductive activity. Maximum numbers of ova among planktotrophic species ranged from 78 thousand ova per female in the ophiuroid, *Amphiodia occidentalis*, to 127 million ova per female in the asteroid, *Pycnopodia helianthoides*. Maximum numbers of ova among the species

Figure 61. Diversity of echinoderm larvae among the Barkley Sound fauna. A. Planktotrophic echinopluteus of Strongylocentrotus droebachiensis. B. Unidentified planktotrophic ophiopluteus. C. Planktotrophic brachiolaria of Pisaster ochraceus. D. Lecithotrophic modified brachiolaria of Henricia leviuscula. Photograph by R. Koss. E. Planktotrophic auricularia of Parastichopus californicus. F. Lecithotrophic doliolaria of Psolus chitonoides. Photograph by F. McEuen. G. Lecithotrophic doliolaria of Florometra serratissima. Photograph by R. Koss.


A
B
C
D
E
F
G

with lecithotrophic development ranged from 427 ova per female in the asteroid, *Crossaster papposus*, to 160 thousand in the holothuroid, *Cucumaria miniata*. The maximum numbers of ova among brooding species ranged from 11 in *Amphipholis squamata* to 1,200 in *Leptosynapta clarki* (Table 29).

Intraspecific differences in the number of ova per female were observed between habitats in two species of forcipulate asteroids. Significantly greater numbers of ova were obtained from gravid females of *Pisaster ochraceus* collected from Taylor Island compared with females from Grappler Inlet (t = 3.3051, p = 0.0018). The inverse trend was evident for brood counts of *Leptasterias hexactis* where significantly larger broods occurred in Grappler Inlet (t = 4.0274, p = 0.0003). Numbers of ova per female were independent of habitat in *Orthasterias koehleri* (Taylor vs. Bamfield, t = 0.5790, p = 0.5666) and *Patiria miniata* (Bamfield vs. Grappler, t = 0.7141, p = 0.4834). In addition, there were no significant differences in the numbers of ova obtained from gravid females of *Strongylocentrotus franciscanus* collected from 3 different depths at Taylor Island (12 vs. 35 ft, t = 0.1493, p = 0.8821; 35 vs. 54 ft, t = 0.6075, p = 0.5495; 12 vs. 54 ft, t = 0.7654, p = 0.4493).

4. Relationships Between Species Diversity, Life History Traits and Distribution

Relationships between modes of development and habitat parameters were examined by Spearman's and Kendall's tests of rank correlation (Table 31). The proportion of species with planktotrophic development was not significantly correlated with species richness, diversity, exposure or depth (Table 31). In contrast, the proportion of species with lecithotrophic development was positively correlated with species richness, diversity, and depth, and negatively correlated with habitat exposure. Brooding species showed an inverse trend and were negatively correlated with species richness, habitat diversity and depth, and positively correlated with exposure. The high frequency of brooding species in intertidal and shallow subtidal habitats is primarily due to the distribution patterns of Leptasterias hexactis and Leptosynapta clarki (See Tables 27 and 28).

Although there were differences in the relative degree of exposure between Taylor Island and Bamfield and Grappler Inlets (Figure 54), comparisons of life history patterns made along the entire exposure gradient within Barkley Sound are misleading because they combine trends within outer coast and estuarine habitats. Correlations that include the entire range of species richness, species diversity and depth values are valid because these parameters are distributed heterogeneously among the 17 transects (see Tables 26 - 28, Figure 59).

Figures 62 and 63 show that the distribution of echinoderms with planktotrophic, lecithotrophic and

TABLE 31

Summary of comparisons between life history traits and species richness, diversity and exposure. Exposure values are dissolution rates of plaster casts. Table entries show results of Spearman's and Kendall's rank correlations and their associated probability values. Probability values > 0.05 are listed as not significant (n.s.). Sample size is 17 for all comparisons except Ova Diameter X Depth (n=36).

COMPARISON	SPEARMAN'S rho	p	KENDALL'S tau	p
Diversity (Hn) X # Species	0.6215	0.001	0.5114	0.005
Diversity (Dn) X # Species	0.5760	0.010	0.4362	0.010
Diversity (Hn) X Exposure	-0.6511	0.005	-0.5092	0.005
Diversity (Dn) X Exposure	-0.6266	0.005	-0.4945	0.005
No. Species X Exposure	-0.2426	n.s.	-0.2340	n.s.
No. Species X Depth	0.1313	n.s.	0.1369	n.s.
% Planktotrophy X # Species	-2.993	n.s.	-0.2491	n.s.
% Planktotrophy X Diversity (Hn)	0.1815	n.s.	-0.1255	n.s.
% Planktotrophy X Diversity (Dn)	-0.0564	n.s.	-0.0812	n.s.
% Planktotrophy X Exposure	0.1202	n.s.	0.0741	n.s.
% Planktotrophy X Depth	-0.2985	n.s.	-0.2090	n.s.
% Lecithotrophy X # Species	0.6204	0.005	0.4886	0.005
% Lecithotrophy X Diversity (Hn)	0.6331	0.005	0.4777	0.005
% Lecithotrophy X Diversity (Dn)	0.5347	0.025	0.4329	0.010
% Lecithotrophy X Exposure	-0.5437	0.025	-0.4270	0.010
% Lecithotrophy X Depth	0.6724	0.005	0.4906	0.005
% Brooding X # Species	-0.4414	0.050	-0.3422	0.050
% Brooding X Diversity (Hn)	-0.6077	0.010	-0.4684	0.010
% Brooding X Diversity (Dn)	-0.5242	0.025	-0.3941	0.025
% Brooding X Exposure	0.4435	0.050	0.2687	n.s.
% Brooding X Depth	-0.7921	0.001	-0.6316	0.005
Ova Diameter X Depth	0.3876	0.025	0.2799	0.010

Figure 62. Shifts in the proportions of the echinoderm fauna composed of planktototrophic, lecithotrophic and brooding species along the exposure gradient at Taylor Island. Exposure rank values are based on the average rank given to each transect line by the relative weight loss of plaster casts (see Table 26). The numbers above each set of bars indicate habitat depth.

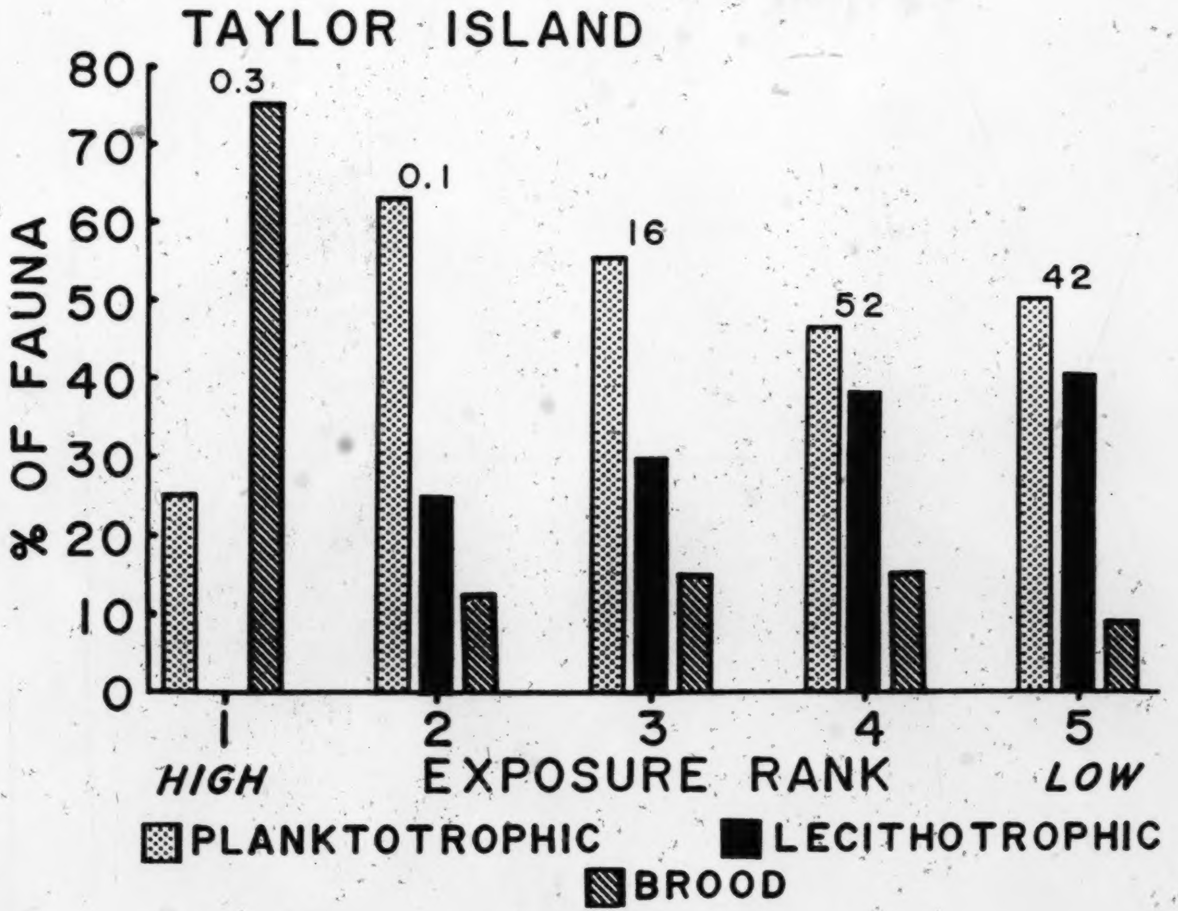
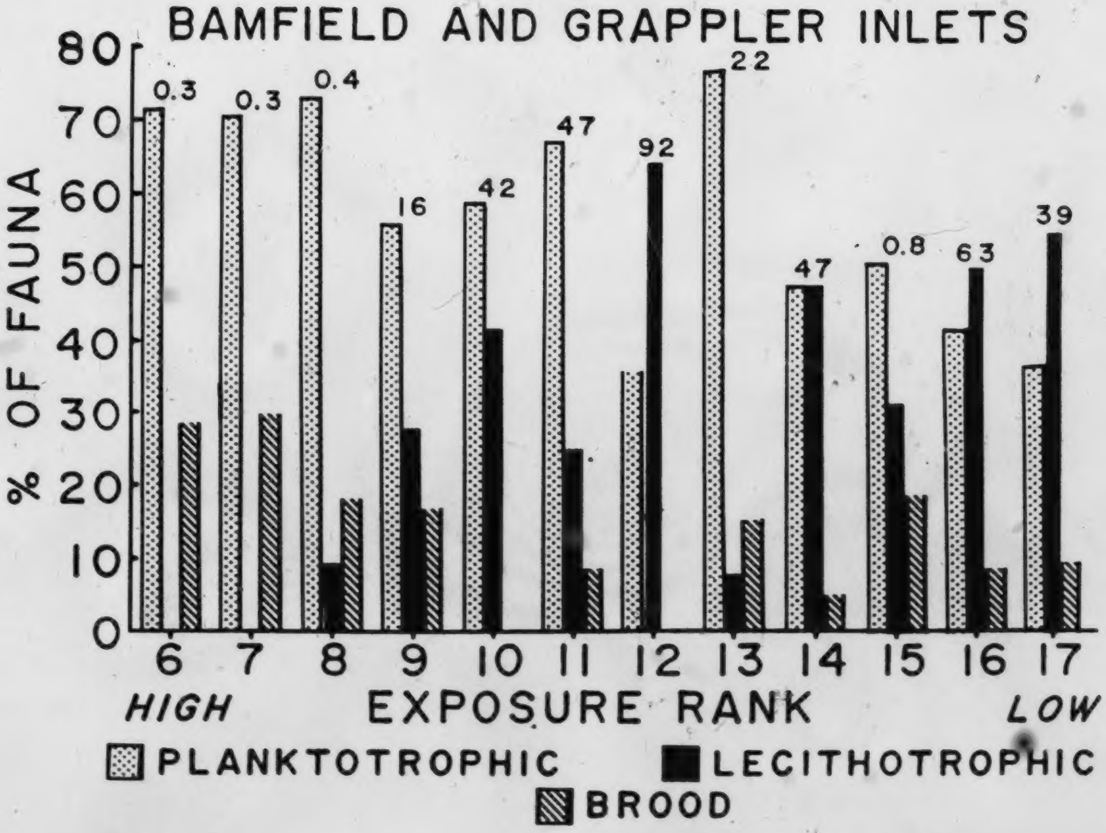

TAYLOR ISLAND
% OF FAUNA
80
70
60
50
40
30
20
10
0
0.3
0.1
16
52
42
1
2
3
4
5
HIGH
EXPOSURE RANK
LOW
▨ PLANKTOTROPHIC
■ LECITHOTROPHIC
▨ BROOD

Figure 63. Shifts in the proportions of the echinoderm fauna composed of planktototrophic, lecithotrophic and brooding species along the exposure gradient at Bamfield and Grappler Inlets. Exposure rank values are based on the average rank given to each transect line by the relative weight loss of plaster casts (see Table 26). The numbers above each set of bars indicate habitat depth.


BAMFIELD AND GRAPPLER INLETS
% OF FAUNA
80
70
60
50
40
30
20
10
0
0.3
0.3
0.4
16
42
47
92
22
47
0.8
63
39
6
7
8
9
10
11
12
13
14
15
16
17
HIGH
EXPOSURE RANK
LOW
PLANKTOTROPHIC
LECITHOTROPHIC
BROOD

brooding modes of development are neither uniform nor random within Barkley Sound. Consistent trends were evident when comparisons were made between transect lines at Taylor Island (Figure 62) and between transect lines at Bamfield and Grappler Inlets (Figure 63). There was a general trend toward an increase in the frequency of species with lecithotrophic development with increasing depth and decreasing exposure. Relationships between depth and habitat exposure were also significant for species that brood their offspring. Although correlations between habitat depth, exposure and the frequency of planktotrophic and brooding species were not significant due to the low number of transects at Taylor Island, the frequency of lecithotrophic species showed perfect negative rank correlations with increasing habitat depth and exposure. Similar changes in the frequency of planktotrophic and lecithotrophic species were evident within Bamfield and Grappler Inlets (Figure 63). The proportion of species with planktotrophic development increased significantly along transects with successively greater exposure (rho = 0.6340, $p = 0.025$), while lecithotrophic species became relatively more abundant in habitats characterized by low exposure (rho = -0.7263, $p = 0.01$). Changes in the frequency of brooding species were not significantly correlated with exposure within Bamfield and Grappler Inlets (rho = 0.4429, $p > 0.05$).

The diameters of echinoderm ova are positively correlated with the depth at which adults reached their maximum abundance (Figure 64, Table 31). The relationship is significant only when data from all 37 species listed in Table 29 are considered (rho = 0.3876, $p < 0.025$). Ova diameters among the four brooding species show a negative correlation with depth, although the vertical range of the two subtidal brooding species extend into the intertidal (see Tables 27 and 28). The similar relationship between ova diameter and habitat depth on small and large geographical scales suggests that mechanisms responsible for the generation of large scale variability may be at least partially explained by analogy with local patterns.

Faunal records and published descriptions of larval development provide sufficient information to compare latitudinal shifts in the life history patterns of asteroids from 4 zoogeographical regions located along the north-east Pacific coast (Figure 65). Planktotrophic species composed about 60% of the fauna between 25 and 45°N (latitude), 47% of the fauna between 45 and 55°N, and 14% of the fauna above 55°N. Conversely, lecithotrophic species composed an increasingly greater proportion of the asteroid fauna between 35 and 65°N. Brooding species averaged about 9% of the fauna between 25 and 55°N and increased to 26% above 55°N.

The latitudinal shift in the frequency of asteroid species with planktotrophic and lecithotrophic development (Figure 65) is similar to the local pattern observed for

Figure 64. Relationship between ova diameter and the habitat where species reach their greatest abundance. Densities of species are provided in Tables 27 and 28. The overall correlation between ova diameter and depth of maximum species abundance is significant (Spearman's rho = 0.3876, $p < 0.025$; Kendall's tau = 0.2799, $p < 0.01$). Trends within planktotrophic, lecithotrophic and brooding species are not significant ($p > 0.05$). Dotted line separates intertidal (left) and subtidal (right) habitats.

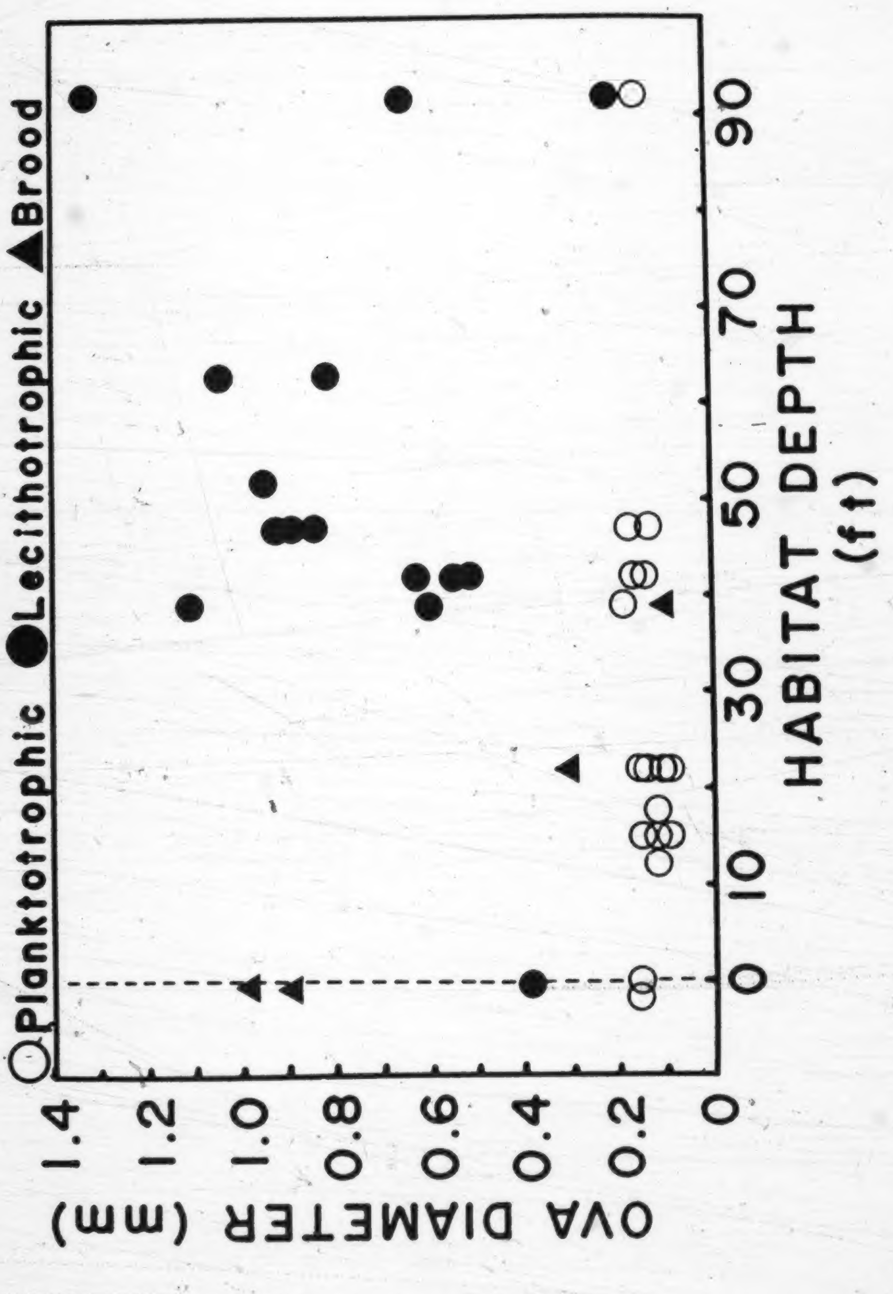
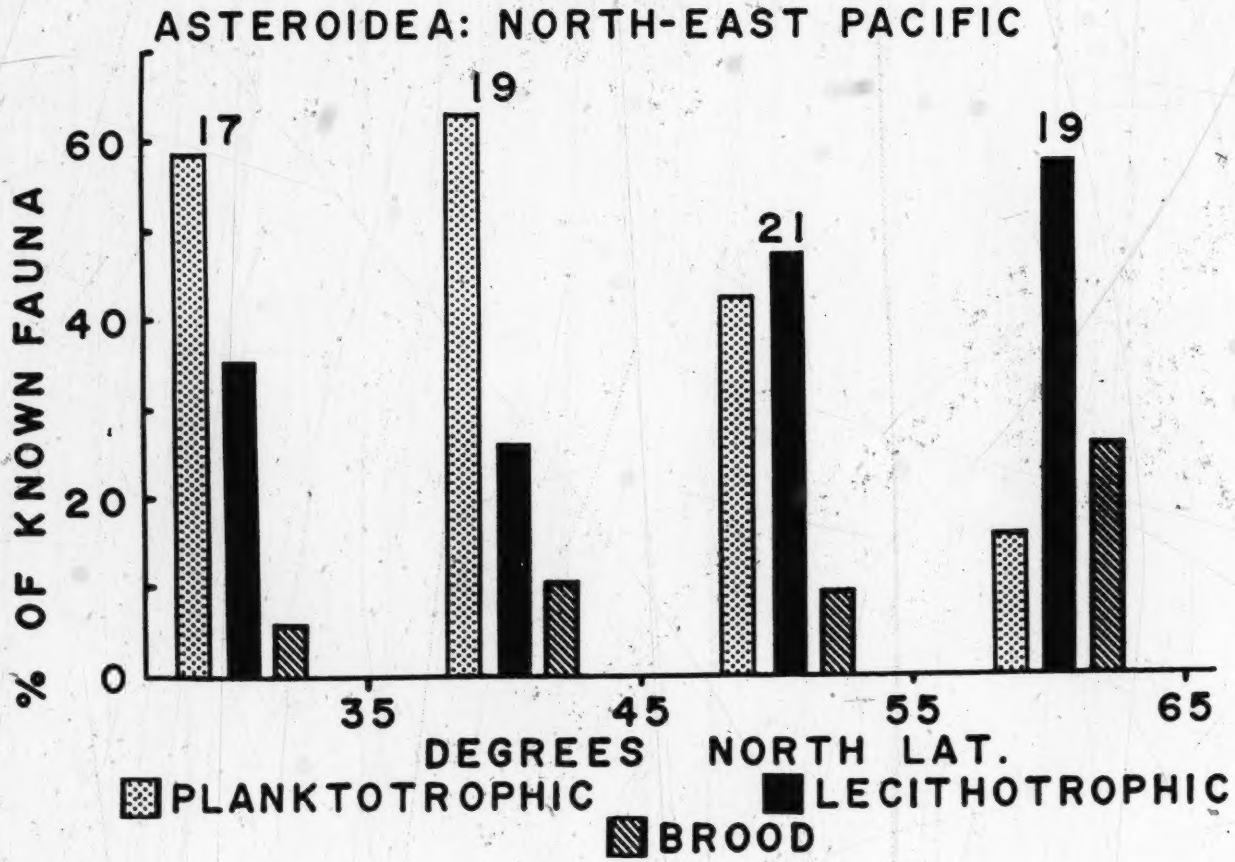

○ Planktotrophic
● Lecithotrophic
▲ Brood
OVA DIAMETER (mm)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
0
10
30
50
70
90
HABITAT DEPTH
(ft)

Figure 65. Latitudinal shifts in the proportions of asteroid faunal assemblages composed of planktotrophic, lecithotrophic and brooding species along the north-east Pacific coast. Descriptions of faunal assemblages were compiled from Verrill (1914), Fisher (1940), McLaughlin (1963), Austin and Deutsch (1978), Feder (1980), and Lambert (1981). Modes of development are listed by Emlet _et al_. (1987). The numbers above the bars indicate the number of species on which the proportions are based.


ASTEROIDEA: NORTH-EAST PACIFIC
% OF KNOWN FAUNA
0
20
40
60
17
19
21
19
35
45
55
65
DEGREES NORTH LAT.
▨ PLANKTOTROPHIC
■ LECITHOTROPHIC
▨ BROOD

echinoderms within Barkley Sound (Figures 62 and 63). Similarity between these large and small scale patterns suggests that geographical shifts in echinoderm life history traits may result from a common mechanism that operates on substantially different spatial scales. An alternative hypothesis is that the geographical patterns in the distribution of echinoderm life history traits may be fortuitous. Detailed information concerning small scale geographical patterns in life history traits are needed for faunal assemblages from other locations to distinguish between these two alternatives.

D. DISCUSSION

Life history traits of echinoderms are traditionally compared according to the morphology and trophic modes of larvae (Chia, 1974). In the Pacific Northwest, the majority of species reproduce by means of: 1) obligate planktotrophic larvae, which are released in great numbers and feed upon algal cells during the planktonic period, 2) lecithotrophic larvae, which are produced in fewer numbers and do not feed on exogenous materials, or 3) brooded offspring, which can be produced in intermediate or low numbers and whose nourishment for development is generally incorporated within the egg. Other modes of development among echinoderms from the Pacific Northwest include the production of facultative planktotrophic larvae and viviparous development (Strathmann, 1978; Strathmann and

Rumrill, in press). In Barkley Sound, 47% of the echinoderm fauna is composed of species with planktotrophic development, 42% of the species have planktonic lecithotrophic larvae, and 11% of the species brood their offspring.

Latitudinal variability in marine invertebrate life history traits has received widespread attention (Fisher, 1940; Thorson, 1950; Ocklemann, 1965; Spight, 1977, 1981; Clark and Goetzfried, 1978; Hansen, 1980; Jones and Simons, 1983; Jablonski and Lutz, 1983; Emlet et al., 1987). Studies of geographical variability in the life history traits of prosobranch and bivalve molluscs reveal a general increase in the proportion of species with non-dispersive development at higher latitudes. Analogous data have been collected for echinoderms (Ericksen, 1940; Valentine and Jablonski, 1983; McEuen, 1986; Emlet et al., 1987) and several other taxa (Jones and Simons, 1983; Valentine and Jablonski, 1983). Since changes in latitude cannot directly affect the life history patterns of marine invertebrates, differences in environmental parameters that vary with latitude are implicated as the mechanism responsible for shifts in the proportions of faunal assemblages that exhibit particular life history traits. Relationships between life history traits and distribution have not been thoroughly investigated on smaller geographic scales. In addition, trends in life history traits based on latitudinal differences have not been compared among faunal assemblages in which the proportions of planktotrophic, lecithotrophic and brooding species are known.

Thorson (1950, 1965) reported a decrease in the proportion of marine prosobranch molluscs with planktonic larvae and a corresponding increase in the proportion of species with benthic development with increasing latitude within level bottom communities along the temperate Atlantic coast. Mileikovsky (1971) called the phenomenon "Thorson's Rule" and he evaluated several other cases where the proportions of species with planktonic and benthic development changed along a latitudinal gradient (Eriksen, 1940; Ocklemann, 1965). The traditional explanation for Thorson's Rule is that the decrease in the proportion of species with planktotrophic development is related to the short period when phytoplankton are available as a source of food. Menge (1975) pointed out several inconsistencies with Thorson's hypothesis, the most serious of which is that while the number of species with planktotrophic development decreases at higher latitudes, individuals of such species can occur in great abundance. Menge's criticism highlights the importance of considering both species richness and the distribution of individuals within a benthic community in estimates of faunal diversity. Thorson's Rule has recently been interpreted as a mathematical artifact of sampling faunal assemblages from sites positioned at non-random points along the geographical ranges of species with planktonic and benthic development (Jablonski and Lutz, 1983; Lindberg, 1985). Carefully designed sampling programs are necessary to determine the relative importance of sampling biases on latitudinal trends in the proportions of planktotrophic, lecithotrophic and brooding species among assemblages of benthic marine invertebrates.

Transect surveys conducted in Barkley Sound indicate that species with planktotrophic, lecithotrophic and brooding modes of development are distributed heterogeneously among marine habitats. The frequency of species with lecithotrophic development was positively correlated with species richness and with estimates of faunal diversity. Brooding species were negatively correlated with species richness, diversity, and depth, and positively correlated with habitat exposure (Table 31). Changes in the relative frequency of species with planktotrophic, lecithotrophic and brooding modes of development were consistent among the Taylor Island, Bamfield and Grappler Inlets study sites (Figures 62 and 63). Small scale biogeographical patterns observed within Barkley Sound are similar to large scale latitudinal shifts in the life history characteristics of echinoderms (Valentine and Jablonski, 1983; Emlet _et_ _al_., 1987). Similar patterns in the reproductive characteristics of echinoderm faunal assemblages on small and large spatial scales suggests that mechanisms that contribute to the formation and maintenance of variable life history patterns may depend on factors that regulate species richness and diversity.

Several factors influence the frequency of species that have planktotrophic, lecithotrophic and brooding modes of development within Barkley Sound. Probably the most important factor is the type of habitat in which the surveys were conducted. Relationships between habitat and mode of development were influenced by depth and exposure, and they are also linked with substratum characteristics. The use of plaster cast as a measure of current velocity should be viewed with caution because the dissolution rates of plaster casts are dependent upon temperature, susceptibility to abrasion, local flow directions, and inherent variability in the plaster mixture (Muus, 1968; Denny, 1985). However, the plaster casts provided a reliable index of relative habitat exposure within Barkley Sound that was consistent with subjective ranks of exposure and with differences in sediment particle sizes. Correlations between developmental mode and exposure rank were nearly identical to correlations between development mode and depth. The consistently high relative weight loss values at intertidal and shallow subtidal transects provide an indication that these habitats are characterized by persistent wave surge and turbulent flow conditions.

The frequency of species that exhibit contrasting modes of development probably shift seasonally within several habitats in Barkley Sound. For example, individuals of

Pisaster ochraceus are less abundant along intertidal transects during fall and winter months when they migrate subtidally. Surveys of transect lines conducted during winter would be expected to show a relative decrease in the frequency of planktotrophic species at the most exposed sites and a corresponding increase at the less exposed shallow subtidal sites. The proportions of planktotrophic and lecithotrophic species are also sensitive to the appearance of rare species. For example, one individual of Pisaster giganteus occurred along a transect line at a depth of 54 ft at Taylor Island. Similarly, a single individual of Pteraster tesselatus occurred at Taylor Island along a transect 35 ft below MLLW. In each case, the proportions of planktotrophic and lecithotrophic species were influenced little by the appearance of rare species because each site was inhabited by relatively large numbers of species (Table 27). However, the influence of rare species would be greater along transects inhabited by few species.

An additional factor that may influence the proportions of planktotrophic and lecithotrophic species within a particular habitat is that the reproductive modes of resident species may be responsive to local conditions that influence survival of their offspring. Stearns (1976, 1977) proposed a bet-hedging model to predict that fewer offspring are favored in habitats where juvenile mortality is highly variable and of greater magnitude than adult mortality. The relatively low number of planktotrophic species encountered along the deep protected transects and within estuarine habitats may be related to high rates of larval and post-larval mortality. For example, planktotrophic echinoderm larvae are generally smaller in size than lecithotrophic larvae, and they rely on elaborate ciliary bands to swim and capture algal cells. Zooplankton samples collected near the bottom showed that the abundance of predatory demersal zooplankton is greater within the estuarine habitats in Bamfield and Grappler Inlets compared to Taylor Island. As a consequence, small planktotrophic larval stages may risk greater mortality in the estuaries compared with the more oceanic waters that surround Taylor Island. In addition, the silt substratum and high concentrations of suspended particulate material present in the deep water protected habitats may interfere with feeding and growth of planktotrophic larvae. Presumably, particulate material does not influence the survivorship of lecithotrophic echinoderm larvae. Little information is available concerning the mortality rates of pelagic planktotrophic and lecithotrophic larvae. Although differences in larval mortality due to demersal predators and siltation may be partially responsible for differences in the proportion of planktotrophic and lecithotrophic species between Taylor Island and Bamfield and Grappler Inlets, differential larval mortality cannot explain shifts in development mode among the Taylor Island or Inlet study sites.

Previous authors have described correlations between modes of development and depth among bivalves, prosobranch molluscs, and asteroid and echinoid echinoderms (Thorson, 1950; Ockelmann, 1965; Jackson, 1974, Jablonski and Valentine, 1981; Rex and Warén, 1982; Emlet et al., 1987). These studies document a general trend toward increased lecithotrophy with increasing depth among bivalves and echinoderms. An inverse trend was reported for prosobranch gastropods by Rex and Warén (1982), although the trend was largely restricted to a single family (Turridae). Rex and Warén (1982) suggested that the inverse relationship between reproductive mode and depth among turrids may be related to selective pressures that favor the dispersal of offspring in deep sea habitats.

The trend toward increased lecithotrophy with depth among echinoderms from Barkley Sound is consistent with the large scale pattern reported for asteroids and echinoids by Emlet et al. (1987). In Barkley Sound, the frequency of species with lecithotrophic development increased with depth, although brooding species were negatively correlated with habitat depth. The frequency of species with planktotrophic development was not correlated with habitat depth (see Figure 64, Table 31). These relationships are independent of variation in faunal diversity because species richness was not correlated with habitat depth (Table 31).

Processes that affect the distribution and abundance of adult echinoderms can also contribute to small scale biogeographical shifts in the frequency of planktotrophic and lecithotrophic species. In the Pacific Northwest, echinoderms are ubiquitous members of intertidal and subtidal marine invertebrate communities where they can be influential as ecologically dominant or keystone species (Paine, 1974; Estes and Palmisano, 1974; Duggins, 1980, 1981). Echinoderm communities can be influenced by several processes including: 1) predatory interactions and mutual accomodation (Paine, 1966; Mauzey _et al_., 1968; Paine and Vadas, 1969; Paine, 1976; Estes and Palmisano, 1974; Duggins, 1980; Tegner and Levin, 1982; Whitman, 1985), 2) the frequency and intensity of physical disturbance (Paine, 1966; Dayton, 1971; Sousa _et al_., 1981), and 3) links between trophic modes and habitat heterogeneity (Menge and Sutherland, 1976). Differences in the distribution and abundance of echinoderm populations can also result from variation in the spatial patterns and intensity of settlement events (Keough and Downes, 1982; Gaines and Roughgarden, 1985). Processes that influence temporal and spatial variability in settlement are particularly important because settlement events establish the initial distribution patterns upon which subsequent processes can act (Birkeland and Chia, 1971; Cameron and Schroeter, 1980; Tegner and Dayton, 1981; Young and Chia, 1982; Connell, 1985).

In spite of the enormous complexity of interactions that regulate the abundance an composition of echinoderm communities within Barkley Sound, the proportions of lecithotrophic and brooding species changed predictably with depth and exposure. However, shifts in the frequency of lecithotrophic and brooding species were also influenced by factors that regulate species richness and faunal diversity. In contrast, the frequency of species with planktotrophic development was independent of species richness and faunal diversity. These relationships indicate that care must be exercised to sample faunal assemblages from habitats characterized by similar depth and exposure, and that are represented by comparable numbers of species and faunal diversity.

Results from this investigation suggest that the relative frequency of echinoderms that exhibit planktotrophic, lecithotrophic and brooding modes of development vary along latitudinal, depth, exposure and substratum gradients due to differences in species richness and faunal diversity. Since the life history traits of other benthic marine invertebrates also vary along latitudinal and depth gradients, it is predicted that their patterns of life history diversity may also be correlated with geographic variability on smaller spatial scales.

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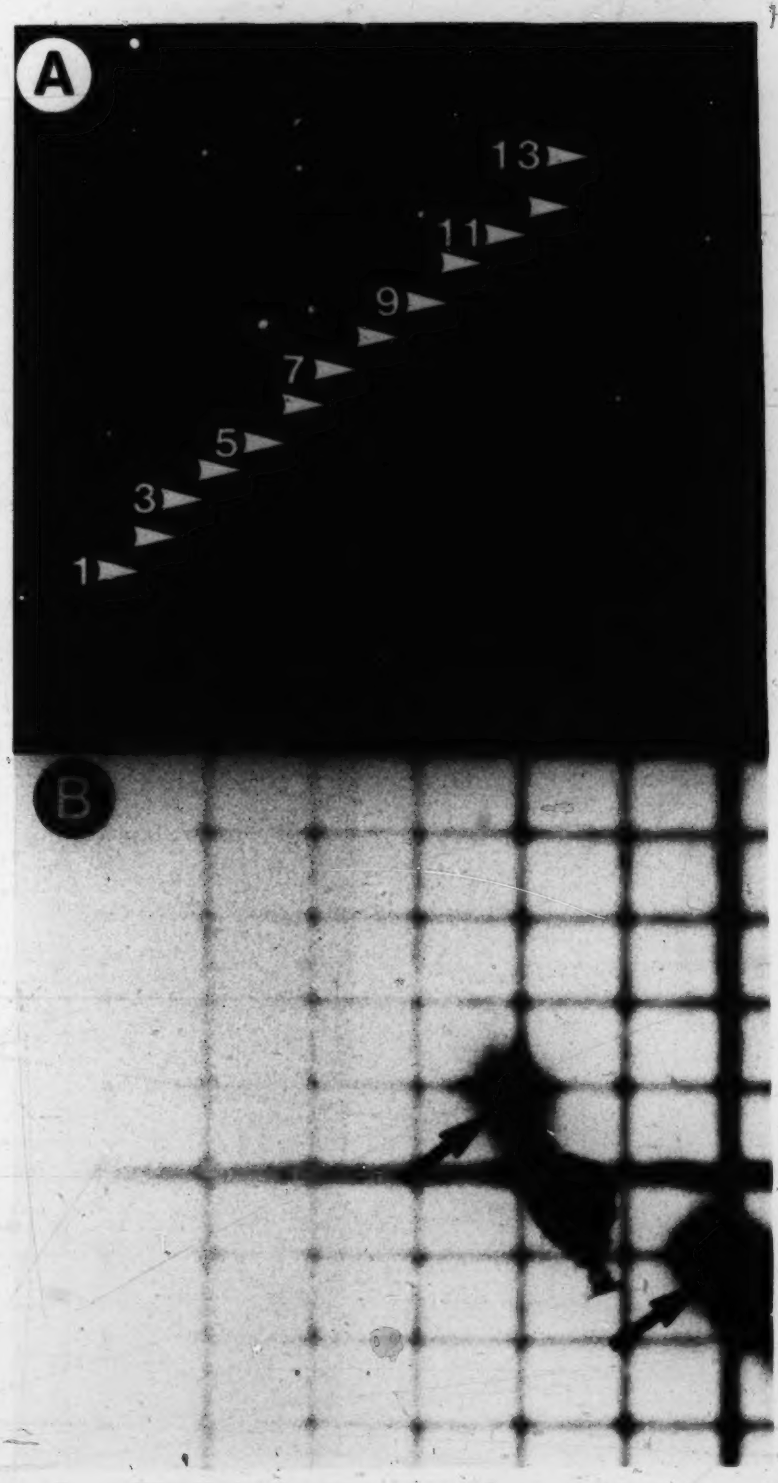
Appendix II. A. Stroboscopic photograph of a Pugettia producta stage I zoea. Arrows and numbers indicate successive images of the zoea over a period of 4 seconds. Instantaneous velocities and acceleration values are obtained by measuring the distances between successive images of the swimming zoea. B. Shadow triangulation of a stage I zoea in an observation chamber. Arrows point to twin shadows created by light directed at the center of the chamber through fibre optic glass. Grid = 1 mm.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